# publications of the INSTITUTE of MARINE SCIENCE

Volume 11 / November, 1966

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Institute of Marine Science
The University of Texas
Port Aransas, Texas

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# Survival of T Bacteriophages and Coliform Bacteria in Sea Water

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## Abstract

Samples taken from four stations in Nueces Bay, Texas, where Portland's sewage treatment plant effluent is discharged were shown to contain various concentrations of coliform bacteria and T bacteriophages.

The 50 percent probability of coliform bacteria was found to be 100 times more than the number of T bacteriophages in polluted areas. In less polluted areas, the ratio was 1 T particle to 10 coliforms.

Because die-off of coliform bacteria and T bacteriophage has been shown to be similar and the detection method is simple, T bacteriophage shows excellent promise of serving as an indicator of marine domestic pollution. Further studies were indicated.

## Introduction

The degree of marine pollution along the coasts is constantly becoming more serious. The contribution of industrial wastes acts as a booster to domestic sources of wastewater which are discharged to the sea at the same time. Techniques for the examination of sea water for pollution have improved little during the last few years. The common denominator used to define and evaluate marine pollution is expressed in standard methods and recommendations of the American Public Health Association (APHA, 1960, 1962). Studies made on streptococcal counting (Burman, 1964; Rose and Litsky, 1965) or the Most Probable Number (MPN) method for *E. coli* (Beck, 1964) have affected improvements in techniques and methods but these have not yet affected the standard procedures (Slanetz, *et al.*, 1964). The academic argument of whether to apply bacteria other than coliform bacteria as pollution indicators has not been solved.

Enteric viruses which are discharged as part of domestic sewage have been found to be relatively resistant to sewage purification processes, and high dosages of chlorine have been shown to be necessary for effective killing of viruses in sewage effluents (Berg, 1964; Clarke and Kabler, 1964; Gilcreas and Kelly, 1955; Kabler *et al.*, 1963).

Mechanisms affecting bacterial die-off in saline water are not well known, though several studies have been performed to gain a better understanding (Carlucci and Parmer, 1959, 1960a, 1960b). The fate of T bacteriophages in sea water is almost unknown, probably because of poor methods for evaluation of small numbers. The method adapted by Carlucci (Carlucci and Parmer, 1960) for small numbers of bacteriophage in large volumes of sea water was a qualitative estimation, and this is probably the reason that no further studies were done.

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The purpose of this study was to follow T bacteriophage mortality in sea water and compare it with coliform bacteria die-off.

## Materials and Methods

*Media.* PABA (Phage Assay Base Agar) purchased from Fischer Scientific Co., was used for all bacteriophage assays. PAB (Phage Assay Base Broth) was used in 10 ml tubes and served for all phage enrichment experiments. The broth consisting of:

| | | |
|---|---|---|
| Beef extract | — | 3.0g, |
| Peptone | — | 5.0g, |
| Sodium chloride | — | 5.0g, |
| Magnesium sulfate | — | 0.2g, |
| Manganese sulfate | — | 0.05g, |
| and Water | | to 1000 ml was mixed and then autoclaved |

at 15 psi, 121 C, for 15 minutes. Before use, 0.15 g/1 of calcium chloride was added to each tube. Buffer dilution water was prepared according to APHA (APHA, 1962). *E. coli B* strain was used for enrichment of bulk T bacteriophages.

*Sampling.* Sea water samples were collected from Nueces Bay, Texas, from Stations 1–4, located 5, 50, 150, and 250 meters, respectively, from Portland's sewage treatment plant discharge ditch. Samples were sent to the laboratory and tested immediately.

*Procedure.* All phage assays were done by the agar layer method described by Adams (1959). For the most probable number of T bacteriophage evaluation, the following procedure was adapted:

1) Each of five tubes containing 10 ml of PAB (Phage Assay Base) broth, double strength, was inoculated with 10 ml of sea water sample.
2) Each of five tubes containing 10 ml of PAB broth, single strength, was inoculated with 1 ml of sea water sample.
3) Each of five tubes containing 10 ml of PAB broth, single strength, was inoculated with 1 ml of 1 to 10 dilution of sea water sample.
4) 0.1 ml of a young culture of *E. coli B* strain containing approximately $10^8$/ml of cells was inoculated to each of these tubes. All the tubes were shaken thoroughly and incubated for 16 hours at 35 C.

Results of the most probable number (MPN) were recorded by transferring a loopful of each of the incubated tubes to freshly inoculated *E. coli B* petri plates. Incubation of this plate containing the transferred samples (from positive tubes) resulted in plaque formation in about six hours. Each plaque represented the appropriate PAB tube in which T phages multiplied. The MPN for T bacteriophage was recorded in the same way as the MPN for coliform bacteria (APHA, 1962). The MPN for coliform bacteria confirmed test was followed as recommended by APHA (1962).

## Results

The number of coliform bacteria at sampling points varied greatly because of the effects of varying weather conditions in altering flow patterns and dilution ratio of the sewage at the sampling points. As expected, in this unfavorable environment, the number

of coliform bacteria decreased, as indicated in Table 1. At most unfavorable conditions, only 2.15 percent of coliform bacteria survived at Station 4; at the same point, 4.73 percent of T bacteriophage survived. At best decay conditions, the survival of coliform bacteria was 0.003 percent, compared with 0.005 percent of T bacteriophage.

TABLE 1

Decay of Coliform Bacteria and T Bacteriophages in the Marine Environment

| Microorganism tested | Percent Survival Compared Between Stations 1 and 4 | |
|---|---|---|
| | Maximum[a] | Minimum[a] |
| Coliform bacteria | 2.15 | 0.003 |
| T bacteriophages | 4.73 | 0.005 |

[a] The results given are based on at least five samples.

Figures 1–4 are probability graphs (Velz, 1951) which show that the ratio at 50 percent probability of coliform bacteria to T bacteriophage was one particle of bacteriophage to 100 coliform bacteria; at Station 3 (Fig. 3), the ratio was 1 T phage particle to 10 coliform bacteria; and at Station 4 (Fig. 4), the ratio was 1 to 16. The relatively parallel lines obtained between the coliform bacteria and T bacteriophage in Figs. 1–4

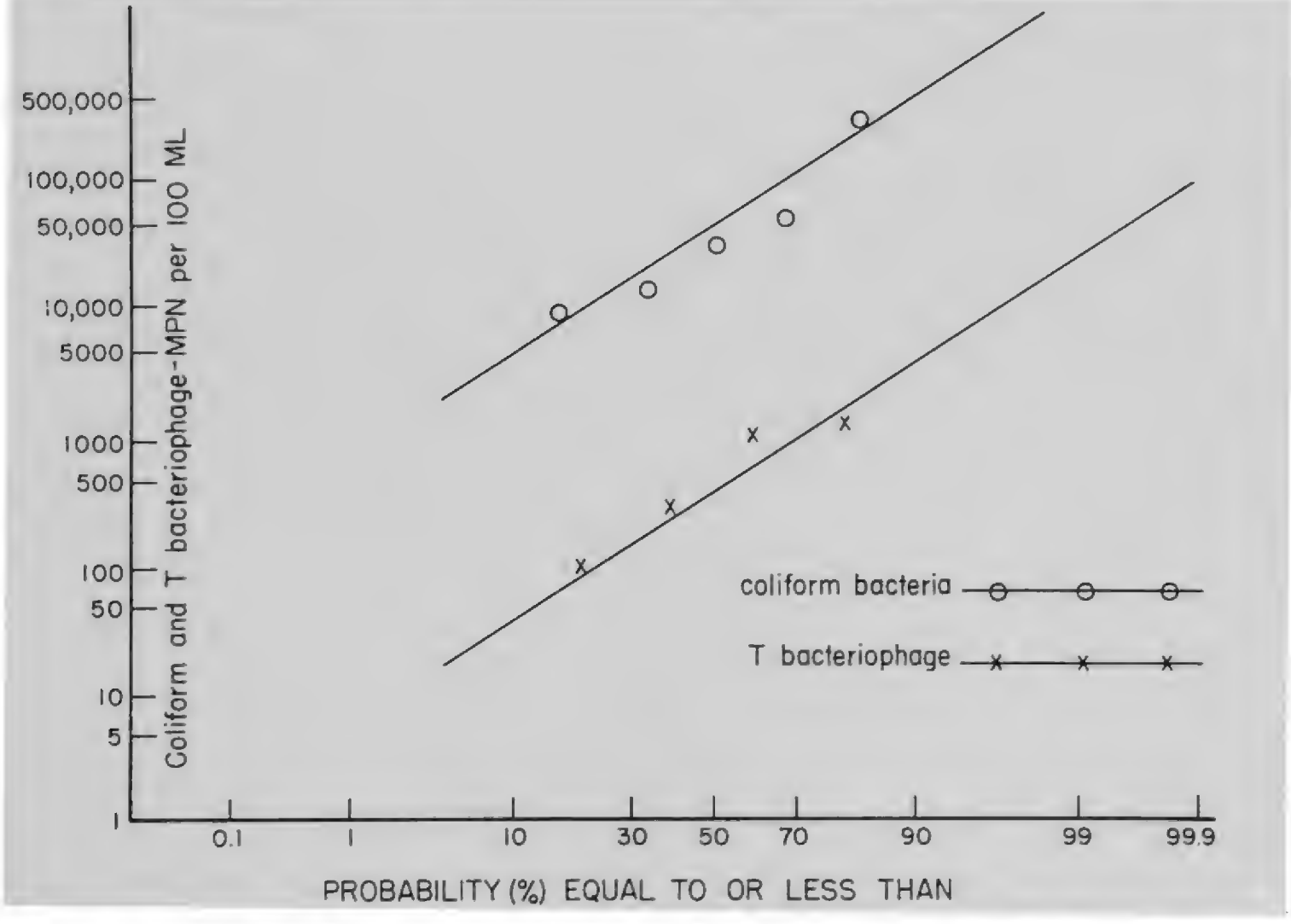


FIG. 1. Comparison of MPN coliform bacteria and T bacteriophage at Station 1, Nueces Bay, 5 meters from Portland sewage discharge ditch.

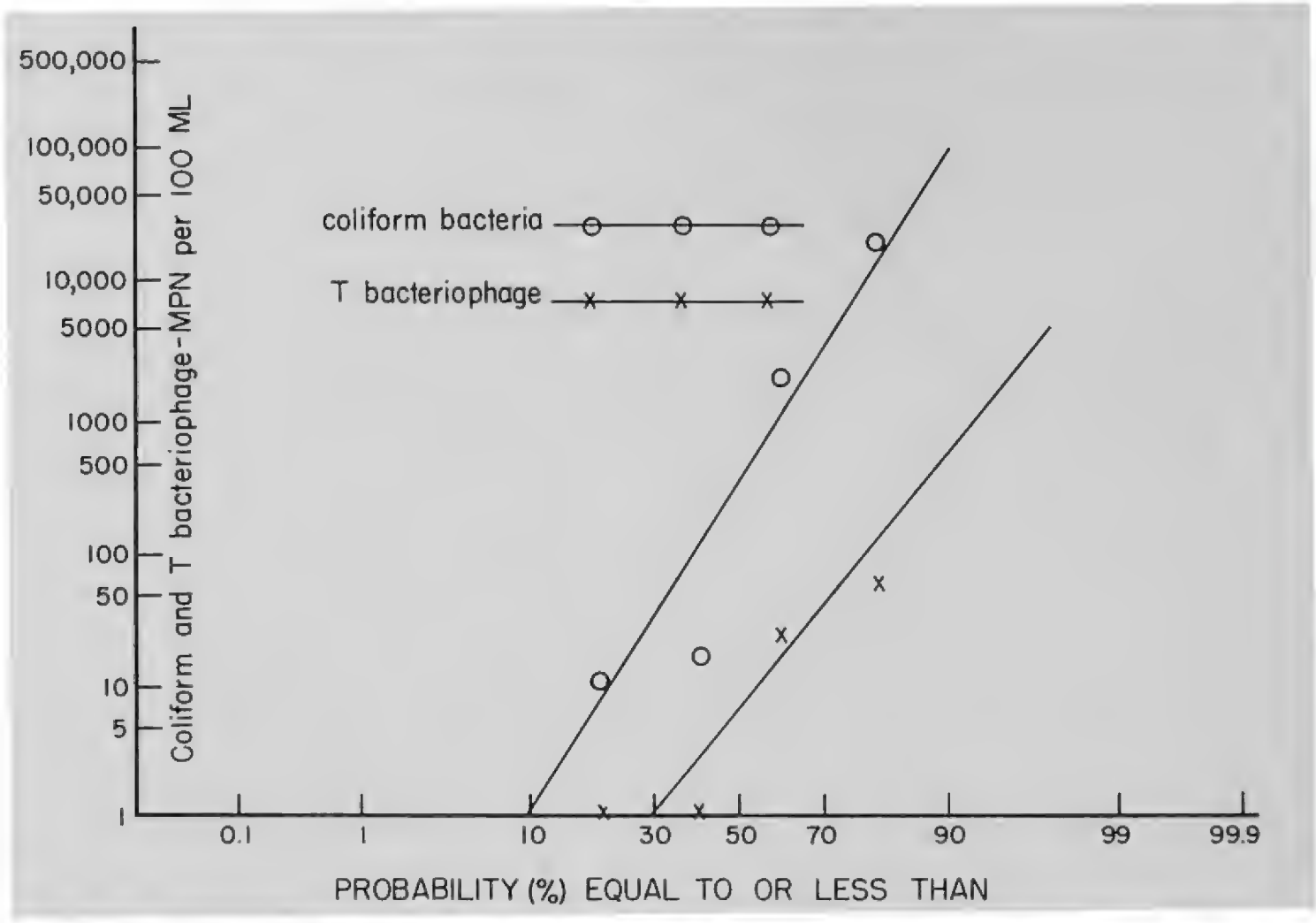


FIG. 2. Comparison of MPN coliform bacteria and T bacteriophage at Station 2, Nueces Bay, 50 meters from Portland sewage discharge ditch.

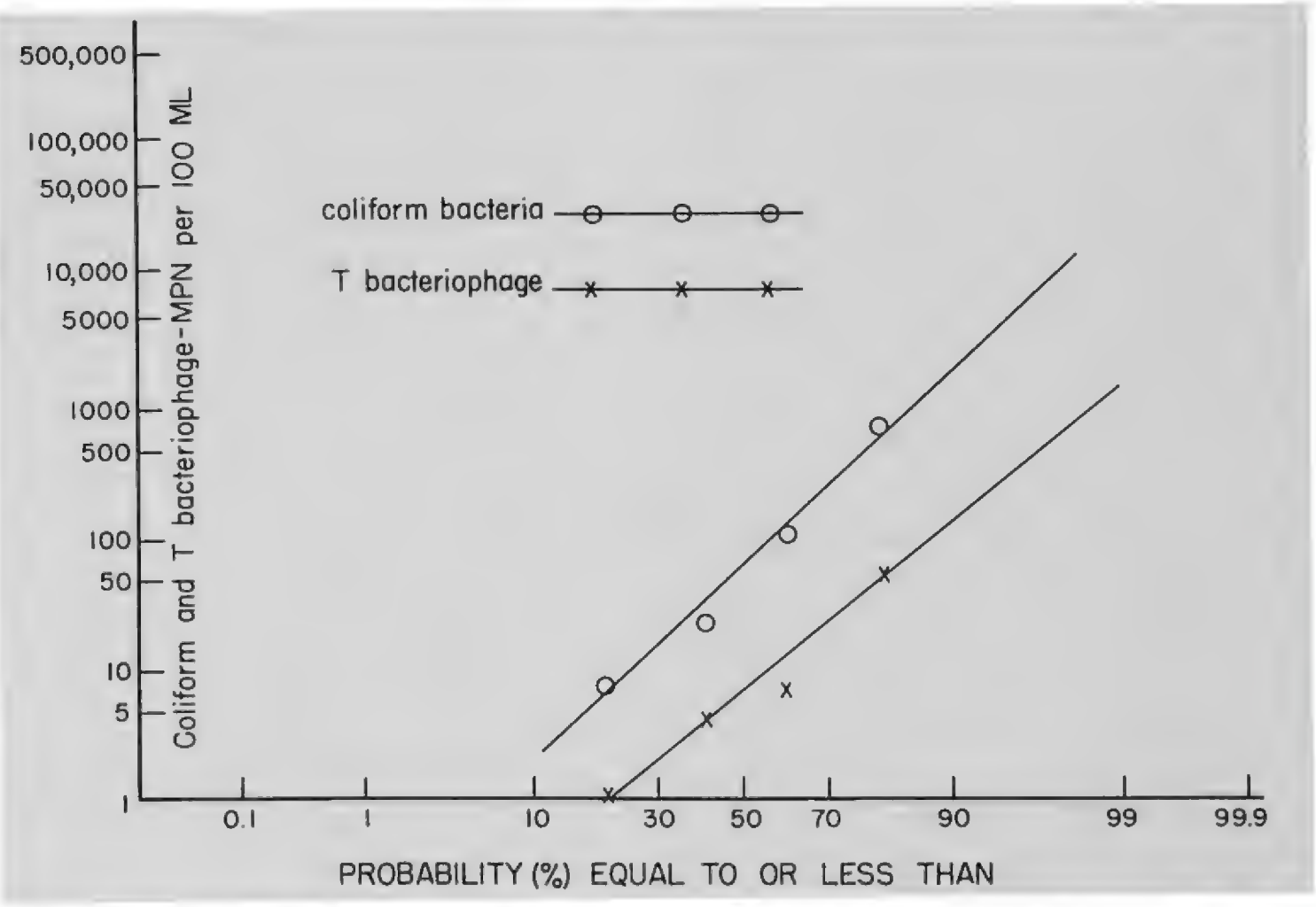


FIG. 3. Comparison of MPN coliform bacteria and T. bacteriophage at Station 3, Nueces Bay, 150 meters from Portland sewage discharge ditch.

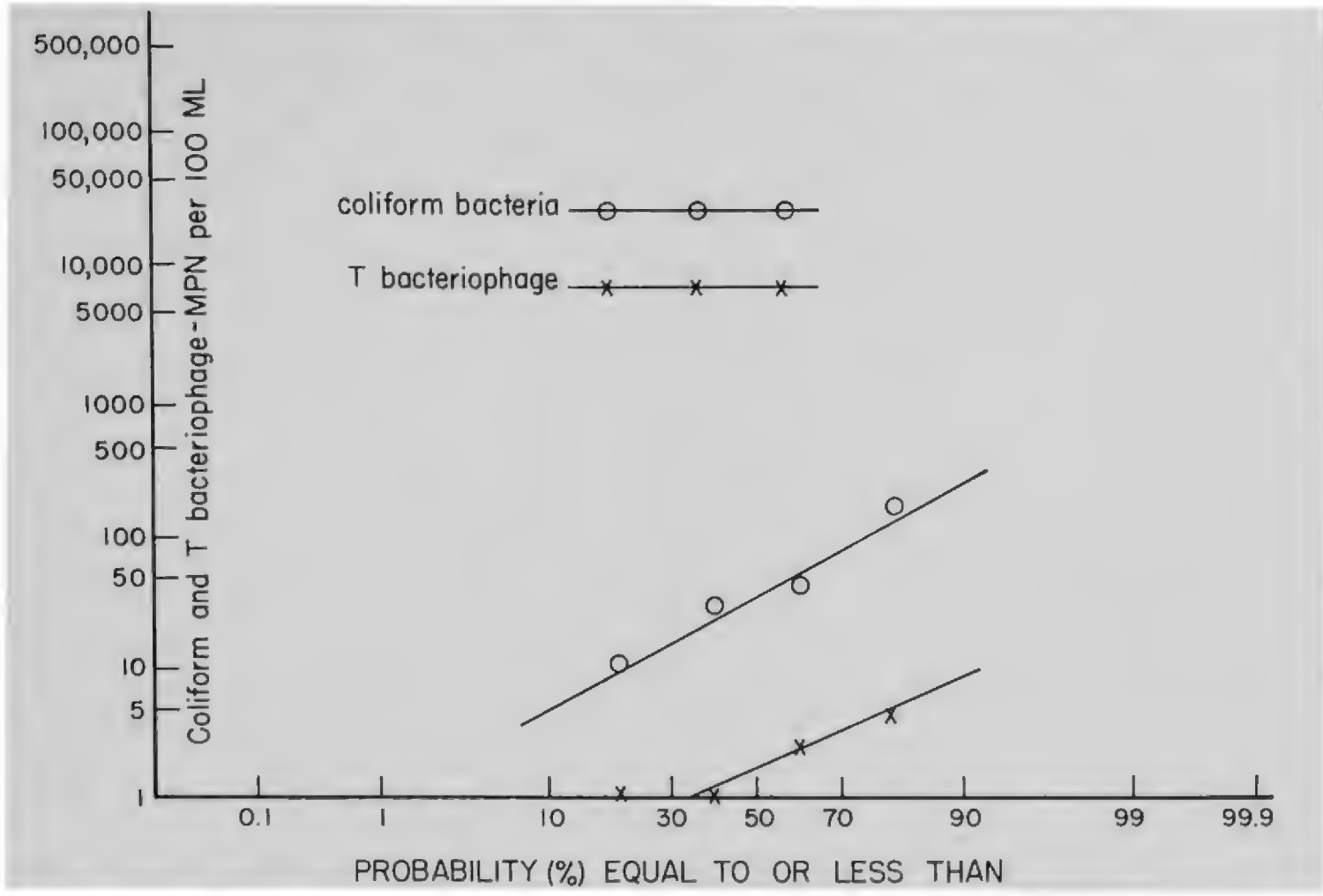


FIG. 4. Comparison of MPN coliform bacteria and T bacteriophage at Station 4, Nueces Bay, 250 meters from Portland sewage discharge ditch.

indicate that the general pattern of the rate of decay of coliform bacteria is equal to die-off of T bacteriophage.

## Discussion

Various studies comparing coliform with other enteric bacteria die-off in saline water, indicate that although coliform MPN is accepted and used as a standard test for evaluation of marine pollution, the resistance of the various species of bacteria to conditions in the marine environment differ significantly. As a result it has been pointed out that the universally practiced coliform MPN test does not truly reflect the enteric bacteria pollution of such waters. The precise tests for *E. coli* and *Streptococcus fecalis* do not permit immediate evaluation of marine pollution and still have not been accepted as alternatives to conventional coliform MPN.

T bacteriophages are natural particles found in sewage, but their pattern of survival in sea water has not been established. Past studies have shown that bacteriophage multiplied in small vessels containing *E. coli* (Carlucci and Parmer, 1960c). In the present study, a steady decline in phage numbers is shown in field experiments. The curves in Figs. 1–4 show that the mortality of coliform bacteria and T bacteriophages is almost parallel. In an area with relatively high pollution, the ratio at 50 percent probability will be 1 phage particle to 100 coliform bacteria. In an area containing approximately 100 coliform bacteria in 100 ml, the ratio will be 1 phage to 10 coliform bacteria.

This study shows that the use of the MPN technique for evaluation of small numbers of

T bacteriophage has the advantage of easy performance over coliform MPN. Additionally, inasmuch as the final results were recorded within 24 hours from inoculation, the time required to do these tests is less. Because T bacteriophages are a part of domestic sewage discharged into sea water, it is likely that adaptations of this assay to evaluate marine pollution will be an improvement over old techniques. It is hoped that this study will stimulate others to further investigation of the relationship between the coliform bacteria and T bacteriophage die-away pattern in various marine environments.

## Acknowledgments

The author wants to acknowledge gratefully the encouragement of Dr. E. F. Gloyna, Head of Environmental Health Engineering, University of Texas (Austin), who initiated the research, and Dr. B. J. Copeland of the Institute of Marine Science, University of Texas, Port Aransas, without whose assistance and guidance this study could not have been undertaken.

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Velz, C. J. 1951. Graphical approach to statistics—evaluation of bacterial densities. Wat. Sewage Wks. 98: 66–73.

# Habitat Segregation in Aquaria Between Two Sympatric Species of *Gobiosoma*

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## Abstract

Habitat segregation between two closely related species of gobies, *Gobiosoma bosci*, and *G. robustum*, was demonstrated in aquaria divided into combinations of three habitat types (oysters, bare sand, turtle grass). *G. bosci*, which lives mainly with oysters, preferred oysters to other habitats and did not occupy turtle grass when oysters were absent. *G. robustum*, which occurs in grass flats, also preferred oysters, but when oysters were absent was attracted to turtle grass. *G. robustum* partially vacated oysters when *G. bosci* was present, and more *G. bosci* stayed in oysters when *G. robustum* was present.

## Introduction

Two species of the fish genus *Gobiosoma* occur in two specific habitats but the mechanisms separating them are unknown. *G. bosci* (Lacépède) lives with reefs of live oysters, *Crassostrea virginica* (Gmelin), and is sometimes found in a few other habitats (Kilby, 1955; Springer and Woodburn, 1960; also unpublished and others). In contrast, *G. robustum* Ginsburg occurs in vegetation covered flats (Reid, 1954; Springer and Woodburn, 1960; Springer and McErlean, 1961). Near Port Aransas, Texas, *G. robustum* was collected only among the marine spermatophytes *Ruppia maritima*, *Diplantheria wrighti*, *Thalassia testudinum*, and the alga, *Padina*. *G. bosci* was found only among oysters. Only one other goby, *Gobionellus boleosoma* (Jordan and Gilbert), was found in both habitats.

*G. bosci* occasionally occurs in grass beds in the Laguna Madre of Texas and Tamaulipas where oysters are absent, but *G. robustum* is the common goby in collections examined by me and according to the data of H. H. Hildebrand (1958 and personal communication). *G. bosci* is also found in beds of *Zostera marina* in Chesapeake Bay (Hildebrand and Schroeder, 1928), but the known range of *G. robustum* extends only as far north as middle Florida (Ginsburg, 1933). Habitat data for these two species in the past have been misleading, partly due to confusion of material, but it is now clear that *G. robustum* is the common species in grass beds and *G. bosci* on oysters. Exceptions have been found where beds of oysters grow interspersed with marine grasses.

Although there are many field observations of congeners occupying different habitats, few studies investigate possible isolating factors. Delco (1962) showed that the shiner, *Notropis lutrensis*, preferred open current and *N. venustus* shelter, corresponding to their distribution in streams. Clark Hubbs (1960) noted that the darter *Etheostoma lepidum* prefers vegetated riffles and *E. spectabile* open riffles where the species are sympatric. Where they are allopatric, their habitat preference seems more general, parallel to the

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present case of *Gobiosoma*. A similar case occurs in spadefoot toads (*Scaphiophus*) which show more habitat specificity where two species are sympatric (Wasserman, 1957).

## Methods

The two basic habitat types, oysters and turtle grass (*Thalassia testudinum*) were constructed in a 75 gallon aquarium considered to have 3 experimental areas each about 50 cm long, 51 cm wide, with 2575 cm² of area (Fig. 1). A layer of sand about 3 cm deep

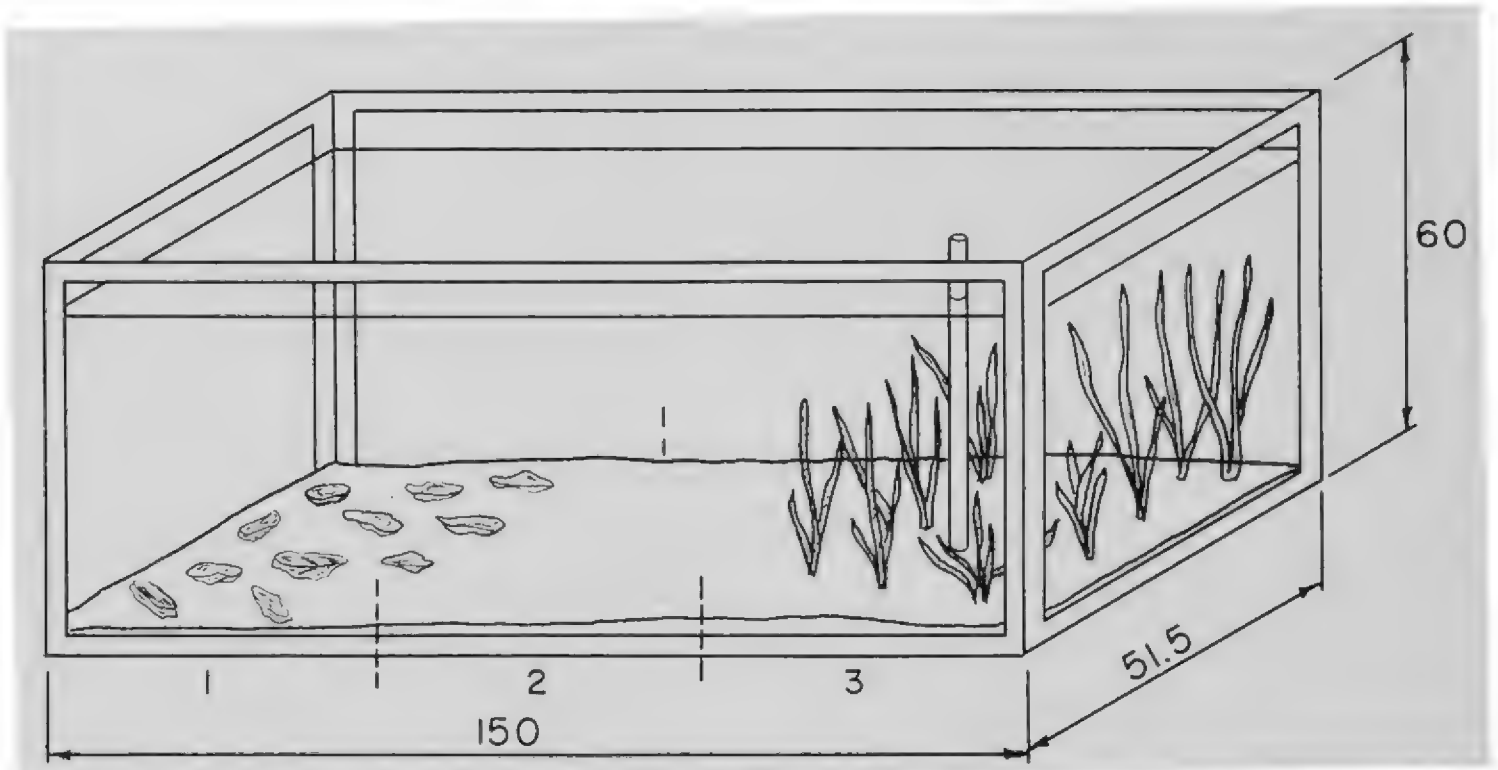


FIG. 1. Aquarium used in preference experiments. Concentrations of oysters and turtle grass were greater than shown. Measurements are in cm.

was laid over the bottom with the oysters and turtle grass inserted in the sand in end compartments. The middle was left bare. About 33–38 live, one-year old Port Aransas oysters (5–7 cm) collected from a boat basin were used to fill the oyster area. An area of turtle grass ⅓ the aquarium size was transplanted from nearby Redfish Bay for experiments involving grass. It was always taken from areas where growth was thickest. A plastic drain pipe was present in the middle of one of the end compartments. Controls were independent of this pipe, and habitat types were alternated between ends to see if the pipe had an influence. No relation between the pipe and distribution of the fish could be detected.

The following combinations were used in the compartments: oysters-sand-sand, oysters-sand-grass, sand-sand-grass, and sand-sand-sand (control). The control tank contained three similar compartments with no habitat types present, except a bare sand bottom. Using both species separately and together gave 12 combinations of species and habitats.

Experimental gobies were taken from a stock of about 30 to 40 of each species (25–40 mm standard length) held separately. Ten specimens of each species were used in most studies, giving a maximum of 20 fish when both species were together. At successive time intervals (15 min or longer multiples) the fish in each compartment were counted. After

a minimum of usually 14 observations these counts were converted to percentages, representing the amount of time each species remained in each compartment. Percentages based on the first ten observations differed little from those after 15 or 20 suggesting the system was stable (Table 1).

TABLE 1

Example of distribution of species with time. Only 11 of 34 records shown. Numbers of each species in each area is shown

| Time | Turtle Grass | | Sand | | Oysters | |
|---|---|---|---|---|---|---|
| | *robustum* | *bosci* | *robustum* | *bosci* | *robustum* | *bosci* |
| 1100 | 15 Aug. placed 10 of each in center | | | | | |
| 1115 | 1 | .. | 1 | 1 | 8 | 9 |
| 1130 | 2 | .. | 2 | 1 | 6 | 9 |
| 1200 | 2 | | 3 | .. | 5 | 10 |
| 1300 | 3 | 2 | .. | .. | 7 | 8 |
| 1315 | 4 | 1 | 2 | . | 4 | 9 |
| 1345 | 4 | 1 | 2 | 1 | 4 | 8 |
| 1430 | 3 | 2 | 2 | .. | 5 | 8 |
| 1600 | 2 | 1 | 1 | .. | 7 | 9 |
| 1900 | 3 | .. | 1 | .. | 6 | 10 |
| 2000 | 4 | 1 | .. | .. | 6 | 9 |
| 2100 | 4 | 2 | .. | .. | 6 | 8 |

Fish were usually observed over a 24-hour period in each combination. All specimens among oysters could not always be seen without probing, so counts were often made only of gobies in grass and sand, all of which could be easily seen.

## Experiments

Even though the individuals in a single compartment area might change, the percentages remained more stable. An example of how the data were compiled which indicates this stability is shown in Table 1. All experiments are summarized in Table 2.

Controls with sand only showed that *bosci* preferred the ends of the tank while *robustum* was evenly distributed. The control percentages were similar for the species separate and combined.

In the oyster-sand-sand combination both species moved to the oysters, and *robustum* kept a higher percentage in oysters than *bosci*. A possible explanation is the tendency for *bosci* to remain in the corners. However, with both species present *bosci* dominated oysters with the same percentage as by itself (62) and *robustum's* percentage dropped to 33, no greater than controls.

With grass-sand-sand *robustum* showed a preference for grass about as strong as *bosci* showed for oysters. When *bosci* was introduced with *robustum*, the *robustum* remaining outside of the grass moved to the center compartment instead of remaining evenly distributed in the other two compartments. This was probably due to dominance of *bosci* in the end compartments. With or without *robustum*, *bosci* showed little deviation from controls.

Oyster-sand-grass produced the most interesting results. Both *bosci* and *robustum* deviated from controls by showing a preference for oysters, but only *robustum* indicated a secondary preference for grass. With both species together a higher percentage (10%) of *bosci* was found in oysters and a few *robustum* (about 10%) moved to the grass.

TABLE 2

Percentages of observations that ten specimens of each species were in each compartment. (S) = Separate, (M) = Mixed

| | | Control | | | | | |
|---|---|---|---|---|---|---|---|
| | | Sand | Sand | Sand | No. Observations | Greatest Variance Between Compartments[a] | Chi Square |
| *robustum* | (S) | 33 | 27 | 40 | 15 | 13% | 1.92 |
| *bosci* | (S) | 45 | 9 | 46 | 15 | 1% | 0.18 |
| *bosci* | (S) | 40 | 5 | 55 | 12 | 15% | 0.84 |
| *bosci* | (S) | 45 | 12 | 43 | 15 | 2% | 0.24 |
| *robustum* | (M) | 35 | 31 | 34 | 14 | 4% | 0.34 |
| *bosci* | (M) | 37 | 9 | 54 | 17 | 17% | 5.17 |
| | | Experimental | | | | Least Variance Between Compartments[a] | |
| | | Oysters | Sand | Sand | | | |
| *robustum* | (S) | 71 | 24 | 5 | 15 | 47% | 104.95 |
| *bosci* | (S) | 62 | 5 | 33 | 19 | 29% | 18.85 |
| *robustum* | (M) | 33 | 47 | 20 | 15 | 13% | 16.58 |
| *bosci* | (M) | 62 | 7 | 31 | 15 | 31% | 17.55 |
| | | Grass | Sand | Sand | | | |
| *robustum* | (S) | 62 | 17 | 21 | 16 | 41% | 60.17 |
| *bosci* | (S) | 40 | 9 | 51 | 15 | 11% | 3.30 |
| *robustum* | (M) | 64 | 27 | 8 | 17 | 37% | 83.55 |
| *bosci* | (M) | 56 | 5 | 39 | 17 | 17% | 5.36 |
| | | Oysters | Sand | Grass | | | |
| *robustum* | (S) | 70 | 7 | 23 | 23 | 47% | 147.81 |
| *bosci* | (S) | 79 | 3 | 18 | 22 | 61% | 85.58 |
| *robustum* | (M) | 59 | 10 | 31 | 34 | 28% | 125.97 |
| *bosci* | (M) | 89 | 2 | 9 | 34 | 80% | 114.3 |
| Switched ends | | | | | | | |
| *robustum* | (M) | 60 | 13 | 27 | 14 | 33% | 63.17 |
| *bosci* | (M) | 82 | 4 | 14 | 14 | 68% | 64.96 |

[a] Since *bosci* consistently avoided the middle, this figure for *bosci* throughout is the difference between end compartments

To see if these distributions were real the oysters and grass were moved to the opposite ends after both species had been in the aquarium for a day. After 5.5 hours in the dark, counts were begun and all percentages were similar. The greatest variance was 7% but most differences were as little as 1 to 4% (Table 2). Since controls varied as much as 17%, it is concluded that these distributions were real and were induced by the habitat and the association with the other species where applicable. Further evidence was an experiment with 10 *bosci* with oysters only in the center compartment and the ends bare. Over 60% remained in the center over a 24 hour period.

Chi-square was computed for each trial for three compartments for *robustum*, and the two end ones for *bosci*. All control values fell well below 0.05 confidence levels, indicating they were a reflection of random distribution of the fish. With two exceptions, all experimental values fell far beyond the 0.01 confidence level. The two exceptions, both for *bosci* in grass, fell at the 0.10 and 0.05 levels, but since one case showed attraction and the other rejection of grass, they mean little. Values for $\chi^2$ became higher as more habitats were introduced, with the highest values from the oyster-sand-grass association.

## Discussion

Correlation of *robustum* with grassy areas and *bosci* with oysters is very good, and occurrence of *bosci* in grass is much less widespread than reported. There are no positive

cases from areas where *robustum* occurs, and where oysters and grass beds are in pure stands. Breder (1942) reported *robustum* from sponge beds, sandy beaches and among mangrove roots. However, Springer and McErlean (1961) failed to find *robustum* in the latter two habitats.

The present observations show that habitat preferences occur in these fishes, and suggest that they are reinforced by meeting the opposite species. Fighting was observed between males of the same and different species as was bowing upward of the head, mouth gaping, and occasional biting and chasing. During these acts the head was very pale, and the body and fins very dark, which contrasts with normally more uniform pigmentation. Both species perceived dialyzed oyster extract, but *bosci* oriented more rapidly. Both species are secretive, and *robustum* resembles dead *Thalassia* leaves; whereas *bosci* is more conspicuous but hides so well among oysters it is seldom seen.

The preceding facts along with the knowledge that *bosci* commonly invades grass flats north of the range of *robustum* (Chesapeake Bay) suggests that these species are separated by competition, especially since the habitat specificity is not absolute.

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# The Plankton of the St. Andrew Bay System, Florida

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## Abstract

Plankton investigations were carried out in 1959–60 and 1961–62 in the St. Andrew Bay System, a complex of shallow estuaries on the north Gulf Coast of Florida. The bay complex is a two-layered system with the vertical salinity gradient averaging 1 ppt near the Gulf to over 9 ppt near the heads of North and East Bays. Mean annual salinity for stations located throughout the bay complex ranged from 19.4 to 32.7 ppt and annual water temperature ranged from 11.5 to 28.8 C.

Samples for phytoplankton and chlorophyll *a* analyses were taken from surface waters and in 1961–62 eight separate diatom genera exceeded 1% of the total diatom volume. In order of importance they were *Chaetoceros*, *Rhizosolenia*, *Skeletonema*, *Cyclotella*, *Thalassiothrix*, *Coscinodiscus*, *Bacteriastrum*, and *Thalassionema*. *Chaetoceros*, *Rhizosolenia*, and *Thalassiothrix* occurred in greatest numbers in relatively high salinities while *Skeletonema* was most abundant at intermediate salinities. Distributional patterns of the other major planktonic genera were somewhat less distinct. Diatom volume increased with increasing salinity whereas diatom numbers were greatest at intermediate stations. Chlorophyll *a* concentrations were highest at stations farthest into the estuaries. The annual mean for surface chlorophyll *a* was 2.13 mg/m$^3$ and means for diatom numbers and volume were $8 \times 10^5$ cells/l and 0.5 mm$^3$/l respectively. Seasonal peaks for chlorophyll *a*, diatom numbers, and diatom volume did not correspond in time.

Zooplankton was collected by oblique tows with Clarke-Bumpus samplers fitted with #10 mesh nets. Zooplankton standing crop in the bay system varied within relatively narrow limits with the largest populations occurring near the head of West Bay and the smallest near the heads of the East and North bays of the system. Average counts and biomass (dry weight) for 1961–62 were 40,100/m$^3$ and 42.7 mg/m$^3$. Seasonal peaks occurred in June of 1959 and in August, September, January, and June of 1961–62. Standing crop minima were recorded for August and February of 1959–60 and for February and April of 1962.

Copepods constituted the most important zooplankton group and accounted for 60% of the zooplankton number and 56% of the dry weight. The two next most important zooplankton groups were larvae of benthic invertebrates and appendicularians. Together these three groups totalled 79% of the zooplankton number and 92% of the dry weight. Other groups seasonally important were rotifers, cladocerans, and *Noctiluca*.

The most abundant zooplankton species were, in order of importance, *Acartia tonsa*, *Paracalanus crassirostris*, *Oikopleura dioica*, *Oithona brevicornis*, *Noctiluca scintillans*, *Oithona nana*, and *Synchaeta* sp. These seven species constituted over 50% of the zooplankton dry weight.

Both diatom and zooplankton diversity increased towards the Gulf with increasing salinity. Zooplankton diversity tended to decrease in winter with the annual low occurring in February but diatom diversity evidenced no clear seasonal trends.

Results of multiple-linear regression analyses indicated that little of the total variance in plankton biomass could be attributed to physical parameters such as salinity and temperature and that there was little correlation between zooplankton and diatom biomass fluctuations. It was suggested that large predators such as scyphomedusae and ctenophores play a major role in regulating microzooplankton abundance in the St. Andrew Bay System.

A comparison of St. Andrew Bay phytoplankton and zooplankton standing crop with that of other areas along the Gulf and Atlantic coasts revealed that St. Andrew Bay standing crop was somewhat less than that of other estuaries but greater than most open sea areas considered.

[1] Based on a Doctoral Dissertation submitted to the graduate school of the Florida State University.

## Introduction

Plankton were collected in the St. Andrew Bay System, Florida from 1959 to 1962. Data are presented on seasonal changes in plankton composition and biomass and on some of the environmental parameters which may have strongly influenced observed biological variations.

Since an understanding of plankton dynamics first requires estimates of standing crop, considerable effort in this investigation was devoted to assaying plankton biomass. Most papers of quantitative data on Gulf of Mexico plankton have expressed abundance in terms of numbers of a plankton species per given volume of water (King, 1950; Pierce, 1951; Grice, 1953; Curl, 1959; Thomas and Simmons, 1960). Grice (1957) estimated volume contributions for individual plankton species, but only for copepods. The St. Andrew Bay program attempted to assay more adequately the contribution of individual species to total standing crop.

## The St. Andrew Bay System

The St. Andrew Bay System (Fig. 1) is a complex of shallow coastal plain estuaries located on the northern Gulf Coast of Florida. The bay complex occupies 90 square miles between longitudes 85° 23′–85° 53′ West and latitudes 30° 00′–30° 20′ North. This system is formed by three estuaries, North, West, and East Bays, which flow into a central basin, St. Andrew Bay. Two of the bays, North and West Bays, merge to form the upper arms of a "Y" before opening into St. Andrew Bay. Centrally located St. Andrew Bay has access to the Gulf through two passes, West Pass to the south and East Pass to the southeast. Hypsographic curves (Waller, 1961), show West, North, and East Bays to be comparatively shallow, mean depths being 2.1 m, 1.8 m, and 2.1 m respectively. St. Andrew Bay is deeper, the mean depth being 5.2 m. Sediments of the bay complex were investigated by Waller (1961) who found well sorted sands along the shallow margins and finer grained, more poorly sorted silt-clay sediments in the central troughs.

Ichiye and Jones (1962), in a paper on the hydrography of the St. Andrew Bay System, state that North, West and East Bays are positive estuaries according to Pritchard's (1952) classification in that drainage inflow exceeds evaporation. This results in a net inflow of saline water along the bottom towards the heads of the estuaries and a net outflow towards the Gulf of less dense surface water. St. Andrew Bay itself, having direct access to the Gulf, contains water which is only slightly less saline than coastal Gulf water. Vertical stratification of the water column is generally greatest at points farthest from the Gulf where surface salinities are comparatively low as a result of fresh water discharge. Exceptions can be found in regions of West Bay where wind mixing is often effective in destroying vertical stability (Hopkins, 1963). The tidal cycle in St. Andrew Bay is predominantly diurnal and the tidal amplitude averages between 0.3 and 0.6 m. According to Ichiye and Jones (1962) most of the tidal exchange with the Gulf is accomplished through East Pass which accommodates 65 to 75% of the tidal volume. The chief source of runoff into the bay system has been the Econfina River which empties into the head of North Bay. Recently a dam has been extended across North Bay (completed April 1962) approximately one mile north of station N1. The effects of this dam on the hydrography of the bay system await investigation.

## Methods

The St. Andrew Bay complex was sampled monthly in 1961–62 at the eleven stations indicated on the base map (Fig. 1). A preliminary quarterly survey was carried out at eight of the eleven stations (W1, W2, N1, N2, S2, S3, E1, E2) in 1959–60. In 1959–60 oblique plankton tows were made along with hydrographic casts for temperature and salinity determinations. In 1961–62 Secchi disk readings and water samples for phytoplankton and chlorophyll *a* were obtained.

Most of the chlorinity measurements were made by silver nitrate titration though in some instances hydrometers were used.

Phytoplankton samples were obtained from surface water and preserved in a 4% formalin-seawater solution. Slides were prepared for phytoplankton counts by filtering up to 100 cc of preserved sample through 0.45$\mu$ pore diameter membrane filters. The volume filtered depended on the turbidity of the sample. The filters were placed on slides and cleared with immersion oil. Cell counts were made at 300 × magnification with the diatoms in twenty 0.03 mm$^2$ Whipple disk fields being counted. No distinction was made between cells containing chlorophyll and those without. Estimates of cell volume were obtained by measuring the major axes of five of each type of cell (predominantly diatoms) on every slide and substituting these dimensions into simple geometric formulae.

Chlorophyll *a* was extracted and measured in a manner similar to that outlined by Marshall (1956). Up to a liter of water was filtered through 0.80$\mu$ pore diameter membrane filters at 22 psi. The filters were placed in 5 cc of 90% acetone and extracted for at least 12 hours in the dark at approximately 4 C. The samples were centrifuged in a clinical centrifuge to remove undissolved portions of the filters and other debris. The clear supernatant was read at 660 m$\mu$ against a 90% acetone-dissolved filter standard. The amount of chlorophyll *a* in a cubic meter of water was calculated by the following formula (Marshall, 1956):

$$\frac{1.03 \text{ Klett readings} \times \text{vol. extract (ml)}}{\text{vol. sample (l)}} \times 0.034 = \text{mg chl. } a/\text{m}^3$$

Zooplankton was collected by oblique hauls with #10 nylon nets mounted on Clarke-Bumpus samplers. The catch was preserved in a 5% buffered formalin-seawater solution. Counts of smaller microcrustaceans were made on 1/100 or 2/100 of the sample while larger plankters such as thaliaceans, chaetognaths, sergestids, amphipods, ostracods, siphonophores, and hydromedusae were counted in 8/100 aliquots. Tintinnids were so small and on occasion so numerous that in some samples only those in 1/1000 of the total catch were enumerated. All aliquots were taken from samples using the zooplankton subsampler described by Hopkins (1962). The average number of zooplankters counted for each collection was 1216.

Zooplankton biomass was estimated by summing dry weight contributions of each plankton type in a sample. Dry weights of species in sample aliquots were estimated using either a standard species weight based on an average of several weighings, or by using species dimensions vs. dry weight curves. The mean of ten measurements of each plankton type in a sample aliquot was used to obtain dry weight from the curves. Species dry weights were obtained by weighing specimens which were dried on tared cover slips for 12 hours at 70 C. Prior to drying plankters were soaked in several changes of distilled water to remove salt. Weight and dimension data used to construct the curves for

each plankton type except copepods are given in Table 1. Copepod weight curves were constructed utilizing dry weight and cylindrical volume data. Cylindrical volume of copepod species was computed from measurements of metasome lengths and widths. Cylindrical volume averages and dry weights of 67 groups of copepod naupliar and post naupliar stages gave the following regression equations from which copepod dry weights could be estimated:

$$V < 1000: W = 0.0123V + 0.24 \ (r = 0.87)$$
$$V > 1000: W = 0.0192V - 6.70 \ (r = 0.99)$$

where $V$ = volume ($mm^3 \times 10^{-4}$) and $W$ = dry weight ($mg \times 10^{-3}$).

TABLE 1

Dry weight data for various plankters

| Plankter | Sample size | Dry wt per Individual ($10^{-3}$ mg) | Mean Dimension (mm) | Characteristic measured |
|---|---|---|---|---|
| Hydromedusae | 300 | 1.43 | .29 | bell diameter |
| | 45 | 7.33 | 1.07 | |
| | 32 | 17.50 | 1.71 | |
| | 14 | 46.43 | 3.60 | |
| Siphonophores | 66 | 1.82 | .98 | eudoxid, bract or |
| | 22 | 5.00 | 3.00 | nectophore length |
| *Creseis acicula* | 267 | 108.42 | .70 | shell length |
| | 19 | 1.27 | 6.60 | |
| *Euconchoecia chierchiae* | 371 | 1.67 | .49 | valve length |
| | 103 | 4.27 | .75 | |
| | 87 | 12.87 | 1.08 | |
| *Lucifer faxoni* | 66 | 8.48 | 2.61 | anterior tip of |
| | 36 | 20.00 | 4.25 | eye to telson tip |
| | 25 | 59.20 | 6.36 | |
| Chaetognaths | 219 | 1.51 | 2.20 | total length |
| | 88 | 9.77 | 3.90 | |
| | 55 | 21.81 | 5.60 | |
| | 25 | 96.40 | 8.00 | |
| Appendicularians | 500 | .36 | .17 | head length |
| | 168 | 2.62 | .38 | |
| | 125 | 6.48 | .62 | |
| *Dolioletta gegenbauri* | 46 | 6.74 | 1.38 | total length |
| | 13 | 18.46 | 2.30 | (of mixed stages) |
| *Noctiluca scintillans* | 787 | .37 | dimension | |
| Immature ctenophores | 22 | 13.64 | not considered | |
| *Synchaeta* sp. | 1488 | .20 | for *Noctiluca* | |
| | 2200 | .28 | and succeeding | |
| Polychaete larvae | 127 | 3.70 | oragnisms | |
| Gastropod-Pelecypod veligers | 853 | 2.66 | | |
| *Evadne tergestina* | 300 | 1.20 | | |
| *Podon polyphemoides* | 297 | .73 | | |
| | 123 | 1.11 | | |
| *Penilia avirostris* | 120 | 1.67 | | |
| *Hyperia atlantica* | 22 | 25.45 | | |
| Cirriped nauplii | 147 | .88 | | |
| Cirriped cypris | 172 | 5.41 | | |
| Decapod larvae | 106 | 6.13 | | |
| | 83 | 4.70 | | |
| Brachiolaria[a] | 130 | .23 | | |
| | 350 | .29 | | |
| Plutei[a] | 100 | .44 | | |
| *Branchiostoma larvae* | 73 | 4.25 | | |
| Fish eggs | 130 | 8.77 | | |
| Fish larvae | 98 | 6.57 | | |

[a] May be an overestimate

Two regression analyses were appropriate since there was a natural break in the data at a copepod volume of 0.1mm$^3$.

Attempts to obtain dry weight data for tintinnids were unsuccessful. Dry weight for species in this group was roughly estimated by computing the volume enclosed by the mean-sized lorica for a given species, then, assuming a specific gravity of unity, multiplying half the computed volume by 0.2. The computed volume was halved because tintinnids rarely seemed to occupy the entire lorica and the value of 0.2 is a conversion factor (Giese, 1957) for obtaining dry from live weight.

## Sources of Error

Sources of potential error in estimating phytoplankton numbers and biomass include patchiness, methods of sample collection and fixation, and error in counting and measuring cells. No data are available on phytoplankton patchiness in St. Andrew Bay. The principal limitation of the collecting method was that only surface samples were taken. A few preliminary investigations on the phytoplankton vertical distribution suggest that cell counts and volumes from surface samples underestimate mean values for the entire water column. Formalin preservation of phytoplankton undoubtedly resulted in an underestimate of total plant abundance since formalin may destroy small athecate cells.

An effort was made to estimate counting error by repeating the standard diatom counting procedure 15 times on the same filter. Traverses across the filter were arranged so that duplicate counts of the same field were avoided. Results of these counts (Table 2) show that variance decreases as mean number of cells counted increases. This is not a linear relationship and the distribution of the values, particularly those for *Chaetoceros* and *Skeletonema*, suggests that different species show varying degrees of clumping on the filters, presumably because of variations in cell numbers per chain and in cell spination. Differential clumping of cells has been noted by Kutkuhn (1958) in phytoplankton counting chambers as well. The coefficient of variation for the total count for 20 fields was 26%, which is probably an overestimate of diatom counting variability since the mean total of test counts was only half the mean of 1961–62 counts.

In regard to volume measurement errors, complex cell shapes were reduced to simple geometric forms. This simplification, along with errors in actual measurement of major cell axes, may have led to volumetric and consequently diatom biomass errors.

The influence of plankton patchiness and collecting and counting errors on estimates of abundance of copepods, the dominant plankton group in the bay system, has been discussed in detail in an earlier paper (Hopkins, 1963).

TABLE 2

Diatom count variance

| Type of diatom | Mean[a] count for 20 × 0.03 mm$^2$ fields | Coefficient of variation (×100) |
|---|---|---|
| *Bacteriastrum* | 4.3 | 90.0 |
| *Chaetoceros* | 21.2 | 33.0 |
| *Skeletonema* | 52.3 | 38.8 |
| Total diatom count | 94.7 | 26.0 |

[a] Mean computed from 15 sets of traverses (*i.e.*, 15 × 20 fields).

FIG. 1. The St. Andrew Bay System, Florida, showing station locations.

Some data are also available on relative filtering efficiency of nets of different mesh sizes. Filtering efficiency was investigated by making a series of surface tows with new #10 (0.155 mm mesh diagonal) and #20 (0.099 mm mesh diagonal) nets. Four tows were made, two with each net, while circling about a marker in an outboard skiff at normal towing speed. Counts were made on 1/100th sample aliquots and were prorated to numbers/$m^3$. Average catch data for the two nets are presented in Table 3 and differences in catch between the two nets are expressed as percent of total #20 net catch. Assuming that the #20 net filtered out virtually all the plankters listed in Table 3, 46% of the total number of plankters was lost through the meshes of the #10 net. In terms of dry weight, percent lost by the #10 net was about the same (43%), though weight losses were differently distributed. The major numerical losses can be attributed to the small copepods *Oithona brevicornis* (9.7%) and *Paracalanus crassirostris* (4.8%), to cope-

TABLE 3

Comparison of the catch of #20 and #10 mesh nets

| | #20 mean no. per $m^3$ | #10 mean no. per $m^3$ | Loss (% total #20 catch) | #20 mean dry wt (mg/$m^3$) | #10 mean dry wt (mg/$m^3$) | Loss (% total #20 catch) |
|---|---|---|---|---|---|---|
| *Oithona brevicornis* | 23,724 | 10,391 | 9.7 | 11.38 | 7.42 | 3.5 |
| *Paracalanus crassirostris* | 29,886 | 23,263 | 4.8 | 13.75 | 16.75 | —2.7 |
| Other copepods | 5,624 | 5,835 | —0.2 | 4.29 | 6.58 | —2.0 |
| Copepod nauplii | 18,865 | 5,085 | 10.0 | 6.51 | 2.13 | 3.9 |
| Tintinnids | 6,517 | 1,889 | 3.4 | .92 | .24 | 0.6 |
| *Oikopleura dioica* | 27,644 | 18,284 | 6.8 | 10.75 | 7.58 | 2.8 |
| Other holoplankters | 1,173 | 1,212 | ..... | .81 | 2.52 | —1.5 |
| Pelecypod veligers | 18,787 | 2,615 | 11.7 | 49.97 | 6.96 | 38.2 |
| Other larvae | 5,637 | 6,214 | —0.4 | 14.36 | 14.54 | —0.2 |
| Total | 137,856 | 74,787 | 45.7 | 112.72 | 64.71 | 42.6 |

pod nauplii (10%), tintinnids (3.4%), and appendicularians (6.8%), and to pelecypod veligers (11.7%). Dry weight loss was somewhat smaller in each of the above groups and in some categories an even slightly greater dry weight was computed for the #10 net. Pelecypod veligers were responsible for most (90%) of the #10 net loss, though much of the veliger dry weight was composed of inorganic shell crystals. Tintinnid loss was undoubtedly underestimated since most of these are capable of passing through the meshes of both nets.

In light of this series of tows the loss of microzooplankton through the meshes of #10 nets is great and comparatively fine #20 mesh nets would seem to have been more suitable for this survey. However, Yentsch and Duxbury (1956) have shown that on occasions fine mesh nets can clog rapidly and even yield reverse meter readings. Since #10 mesh nets are relatively free from mesh clogging, they were used in routine sampling.

Dry weights reported in this paper are based on preserved material rinsed with distilled water. No conversion factor was applied to relate preserved plankton weight to that of fresh plankton.

## Hydrographic Data

Hydrographic data for the St. Andrew Bay System by station and season are presented in Tables 4 and 5 respectively. As Ichiye and Jones (1962) found in their study

TABLE 4

Physical data for the St. Andrew Bay System (1961–62 average values) according to station

| Station | S3 | S2 | E4 | S1 | E3 | W2 | N2 | W1 | E2 | N1 | E1 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Surface salinity (0/00) | 32.2 | 29.2 | 26.7 | 26.3 | 24.0 | 23.9 | 22.8 | 23.2 | 21.4 | 16.8 | 14.9 |
| Bottom salinity | 33.3 | 33.0 | 32.6 | 32.4 | 29.3 | 28.4 | 30.4 | 26.0 | 25.9 | 26.0 | 24.0 |
| Vertical gradient | 1.1 | 3.8 | 5.9 | 6.1 | 5.3 | 4.5 | 7.5 | 2.8 | 4.5 | 9.2 | 9.1 |
| Mean salinity | 32.7 | 31.0 | 29.7 | 29.2 | 26.9 | 26.2 | 26.2 | 24.6 | 23.7 | 21.4 | 19.4 |
| Mean temperature (°C) | 22.8 | 22.7 | 22.7 | 22.8 | 22.4 | 22.9 | 23.5 | 23.1 | 22.4 | 23.8 | 22.5 |
| Secchi depth (m) | 6.5 | 4.6 | 3.8 | 3.7 | 3.4 | 2.9 | 2.9 | 2.1 | 2.5 | 1.9 | 1.6 |
| Station depth (m) | 11.5 | 11.8 | 12.9 | 15.5 | 6.1 | 4.7 | 5.8 | 5.0 | 3.2 | 2.9 | 4.5 |
| Distance from Gulf (miles from S3) | 0 | 3.0 | 7.0 | 6.4 | 11.7 | 10.4 | 11.0 | 14.7 | 15.5 | 15.0 | 20.4 |

TABLE 5

Seasonal data (average of all stations) on salinity, temperature, and transparency of the St. Andrew Bay System

| Date | Mean salinity (ppt.) | Mean temperature (C) | Secchi depth (m) |
|---|---|---|---|
| Aug '59 | 21.4 | 28.4 | .... |
| Nov '59 | 23.6 | 20.6 | .... |
| Feb. '60 | 23.0 | 15.3 | .... |
| June '60 | 27.3 | 28.0 | .... |
| July '61 | 25.3 | 28.8 | |
| Aug '61 | 24.7 | 28.8 | 4.1 |
| Sept '61 | 23.4 | 28.2 | 2.9 |
| Oct '61 | 27.9 | 25.7 | 4.4 |
| Nov '61 | 30.6 | 21.4 | 3.4 |
| Dec '61 | 29.7 | 19.5 | 2.9 |
| Jan. '62 | 26.0 | 11.5 | 3.2 |
| Feb '62 | 26.8 | 17.3 | 3.7 |
| Mar '62 | 26.8 | 18.1 | 2.9 |
| Apr '62 | 21.3 | 21.3 | 2.1 |
| May '62 | 25.3 | 26.0 | 3.0 |
| June '62 | 28.7 | 27.7 | 3.2 |

of the bay complex, salinity increased with distance from the heads of the bays towards the Gulf with mean annual salinity ranging from 19.4 ppt at E1 to 32.7 ppt at S3. At all stations salinity at the surface was less than bottom salinity. Greatest differences between bottom and surface salinity occurred at the head of North Bay (N1: 9.2 ppt) and East Bay (E1: 9.1 ppt) while smallest differences occurred at the head of West Bay (W1: 2.8 ppt) and near the Gulf (S3: 1.1 ppt).

Though the overall trend was for vertical salinity difference to decrease towards the Gulf, the relationship was not nearly so linear with distance from the Gulf as was decrease in mean salinity. Variations in vertical differences in regions of comparable salinity are the result of the interaction of the effects of station distance from the source of fresh water, with the quantity of runoff, station depth, and degree of exposure to wind. The most important factor affecting vertical stability undoubtedly varies from one location in the bay complex to another and from time to time, depending on the amount of runoff and the wind velocity and direction. For example, the relatively large mean vertical differences at N1 and E1 may have resulted largely from the proximity of these stations to fresh water sources. Vertical stratification at these stations also was enhanced by the narrowness of East and North Bays at these points which effectively reduced wind fetch and attendant turbulence. The small vertical difference found at W1 probably resulted from a combination of factors such as comparatively small runoff into this region of West Bay and its exposure to wind which had considerable fetch from all quarters. The small mean vertical difference recorded for S3 was largely due to its remoteness from the major sources of runoff and its proximity to Gulf sea water.

Seasonally, mean salinity for the bay system was lowest in August and highest in June of the 1959–60 quarterly survey. In 1961–62 mean salinity values were smallest for September and April and largest for November, December, and June.

Temperature differences throughout the bay system at any one sampling were small and mean values for stations varied less than 2 C. Vertical temperature differences were also small and in only nine of 132 sets of surface and bottom samples did the vertical gradient exceed 2 C. Average temperature for the bay system ranged from 11.5 C in January 1962 to 28.8 C in July–August 1961.

Secchi disk readings showed an apparent strong positive relationship with salinity and increased from bay-head areas towards the Gulf. Seasonally transparency was greatest in the St. Andrew Bay System in October and January through March.

## Phytoplankton Distribution by Season and Station

Records were kept on all genera of diatoms, thecate dinoflagellates, and silicoflagellates encountered in the 20 fields examined on each filter. Distribution by station of the principal genera of diatoms is presented in Fig. 2 A–H and in Table 6. In 1961–62 eight separate planktonic genera exceeded 1% of the total diatom volume in surface waters of St. Andrew Bay. In order of importance they were *Chaetoceros* (30.2%), *Rhizosolenia* (27.3%), *Skeletonema* (8.7%), *Cyclotella* (6.6%), *Thalassiothrix* (5.2%), *Coscinodiscus* (3.1%), *Bacteriastrum* (3.0%), and *Thalassionema* (1.0%). The remaining diatoms, averaging 14.9% of the total diatom volume, were predominantly of benthic genera. Of the eight genera mentioned above, *Chaetoceros*, *Rhizosolenia*, and *Thalassiothrix* were of greatest importance at stations of relatively high salinity near the Gulf.

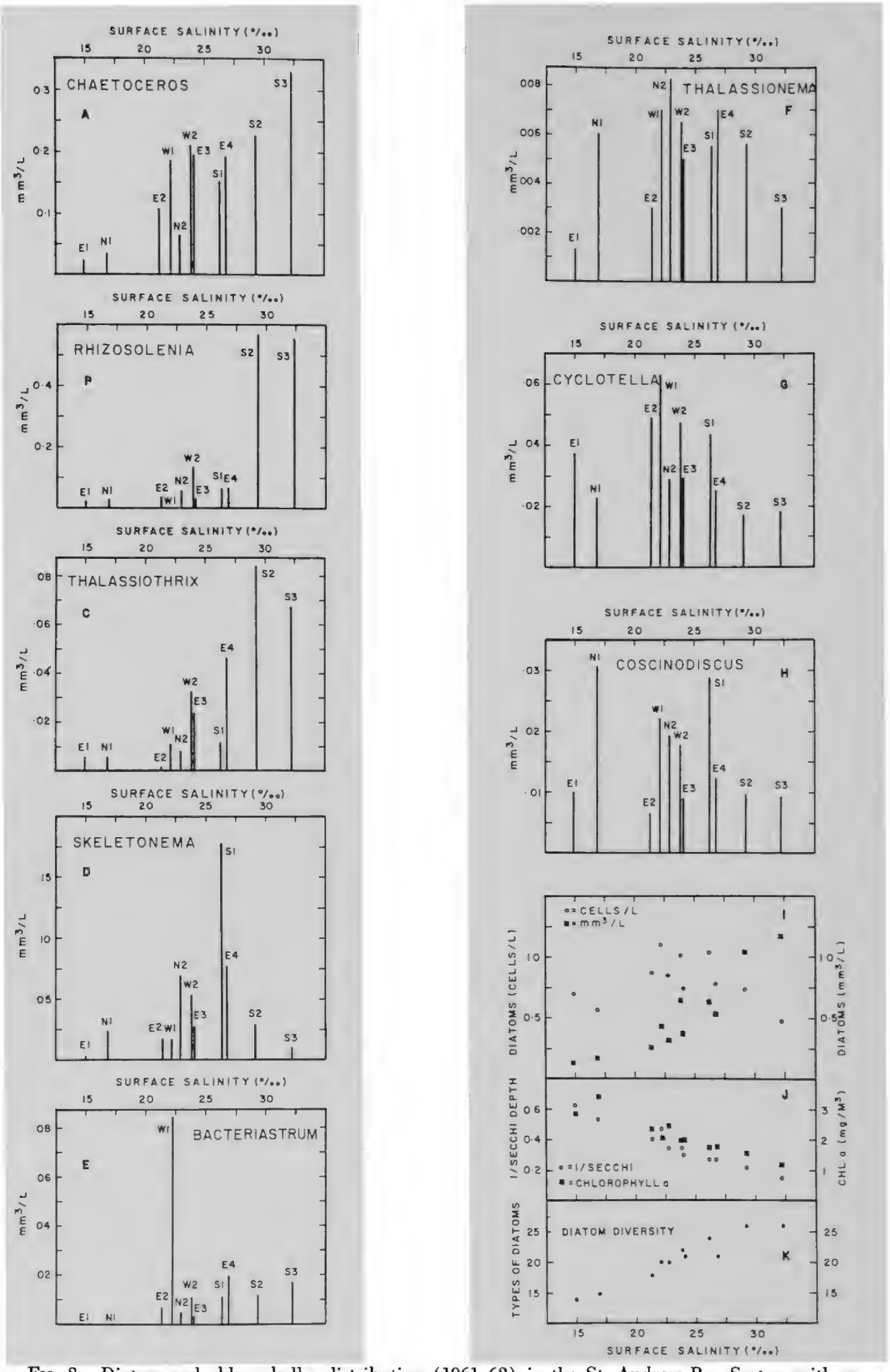


FIG. 2. Diatom and chlorophyll-a distribution (1961–62) in the St. Andrew Bay System with respect to Salinity. A—*Chaetoceros*; B—*Rhizosolenia*; C—*Thalassiothrix*; D—*Skeletonema*; E—*Bacteriastrum*; F—*Thalassionema*; G—*Cyclotella*; H—*Coscinodiscus*; I—Total diatom numbers and volume; J—Chlorophyll-a and 1/Secchi depth; K—Diatom variety.

TABLE 6

Distribution of diatoms and chlorophyll *a* by station in the St. Andrew Bay System (1961–62 average values)

| | S3 | S2 | E4 | S1 | E3 | W2 | N2 | W1 | E2 | N1 | E1 | Avg. | % Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chaetoceros* | .3300 | .2287 | .1947 | .1511 | .1930 | .2094 | .0643 | .1835 | .1092 | .0318 | .0208 | .1560 | 30.2 |
| *Rhizosolenia* | .5585 | .5737 | .0648 | .0639 | .0244 | .1328 | .0581 | 0 | .0336 | .0231 | .0187 | .1411 | 27.3 |
| *Skeletonema* | .0099 | .0289 | .0762 | .1769 | .0251 | .0528 | .0681 | .0153 | .0157 | .0239 | .0003 | .0448 | 8.7 |
| *Cyclotella* | .0180 | .0169 | .0249 | .0433 | .0282 | .0447 | .0282 | .0625 | .0484 | .0225 | .0375 | .0341 | 6.6 |
| *Thalassiothrix* | .0672 | .0839 | .0469 | .0116 | .0244 | .0325 | .0075 | .0107 | .0006 | .0059 | .0054 | .0270 | 5.2 |
| *Coscinodiscus* | .0092 | .0096 | .0123 | .0287 | .0089 | .0176 | .0194 | .0221 | .0063 | .0306 | .009 | .0159 | 3.1 |
| *Bacteriastrum* | .0163 | .0108 | .0191 | .0119 | .0033 | .0114 | .0046 | .0848 | .0061 | 0 | 0 | .0153 | 3.0 |
| *Thalassionema* | .0030 | .0056 | .0070 | .0055 | .0057 | .0065 | .0083 | .0070 | .0029 | .0061 | .0013 | .0053 | 1.0 |
| Rest | .1441 | .0855 | .0923 | .1189 | .0566 | .1360 | .0548 | .0603 | .0316 | .0230 | .0431 | .0769 | 14.9 |
| Total volume ($mm^3/1$) | 1.1543 | 1.0436 | .5382 | .6118 | .3695 | .6436 | .3132 | .4462 | .2544 | .1668 | .1369 | .5162 | 100.0 |
| Total # ($10^6$ cells/1) | .477 | .736 | .771 | 1.048 | .749 | 1.008 | .842 | 1.092 | .860 | .557 | .681 | .802 | . . |
| Types of diatoms | 26 | 26 | 21 | 24 | 21 | 22 | 20 | 20 | 18 | 15 | 14 | . ..... | . .. |
| Chlorophyll *a* ($mg/m^3$) | 1.18 | 1.56 | 1.78 | 1.78 | 1.96 | 1.99 | 2.49 | 2.07 | 2.33 | 3.48 | 2.80 | 2.13 | . . |
| Surface sal (ppt) | 32.2 | 29.2 | 26.7 | 26.3 | 24.0 | 23.9 | 22.8 | 22.1 | 21.4 | 16.8 | 14.9 | ..... | . .. |

Neglecting the unusually high average for W1, *Bacteriastrum* also showed a slight positive trend with increasing salinity. *Skeletonema* was most abundant at stations of intermediate salinity, its greatest volume average occurring at 26 ppt. *Coscinodiscus*, *Thalassionema*, and *Cyclotella* demonstrated less distinct distributional patterns, though the highest values for the latter two genera were recorded for stations intermediate in salinity. Total diatom biomass (Fig. 2 I), on the whole, increased with increasing salinity, the highest average being recorded for S3. Chlorophyll *a* (Fig. 2 J) demonstrated an opposite trend; highest pigment concentrations were found near the heads of bays. This suggests that the importance of the diatom contribution to total chlorophyll *a* in surface waters lessens with distance from the Gulf. Diatom volume and abundance trends were not strongly related since maximum numbers were found at intermediate stations instead of at stations near the Gulf. The mean number of diatoms per liter for the entire St. Andrew Bay System (1961–62) was $8 \times 10^5$.

Diatom variety generally increased with increasing salinity (Fig. 2 K). Greatest average diversity was recorded for S3 and S2, the two stations of highest salinity. Smallest diatom variety was encountered at N1 and E1, stations of lowest salinity.

Table 7 and Fig. 3 A–K contain seasonal data on diatoms, surface chlorophyll *a*, and water temperature. All eight of the principal genera (Fig. 3 A–H) had biomass peaks in summer or fall (*i.e.*, July–November). *Chaetoceros* and *Bacteriastrum* evidenced maxima in June, *Coscinodiscus* and *Skeletonema* in July, *Cyclotella* in August, *Thalassiothrix* and *Thalassionema* in October, and *Rhizosolenia* and *Coscinodiscus* in November. *Thalassiothrix* and *Skeletonema* also had peaks in winter (January and February respectively). No clearly defined maxima were recorded for any of the major genera in spring (March–May).

Seasonally, diatom number and volume and chlorophyll *a* maxima did not correspond well in time (Fig. 3 I–J) and these variables appeared to fluctuate independently of one another. Peaks in diatom numbers (Fig. 3 I) occurred in August, February, and May while diatom volume maxima appeared in November and June. Low values for diatom numbers were recorded for July, November, and January while minima for diatom volume were noted in September and April. The principal chlorophyll *a* peak (Fig. 3 J) was recorded for July and lesser peaks occurred in December and June. Concentrations of chlorophyll *a* were smallest in October and from January through March. Much of the chlorophyll *a* in the St. Andrew Bay System may be detrital, particularly towards the heads of the estuaries, and fluctuations in chlorophyll *a* possibly are related to the amount of detritus in suspension. This argument gains some support in the often inverse relationship between water transparency, as measured by Secchi disk, and chlorophyll *a* values (Figs. 2 J, 3 J). Diatom diversity minima for the bay complex (Fig. 3 K) occurred in September, February, and May while maxima were recorded for August, November, March, and June.

In regard to other thecate groups of phytoplankton, armored dinoflagellates and silicoflagellates were scarce compared to diatoms in the St. Andrew Bay System during 1961–62. *Ceratium* was included in counts of only seven of 132 filters while silicoflagellates (*Dichtyocha*) occurred in counts of 18 filters. When encountered, these cells generally numbered only one cell/20 fields, with three cells/20 fields (*Dichtyocha*) being the maximum. In one instance a chain forming blue-green alga was abundant and in June it constituted 52% of the volume of phytoplankton at station N1.

TABLE 7

Seasonal distribution (average of all stations) of diatoms and chlorophyll *a* in the St. Andrew Bay System in 1961-62

| | 1961 Jul | Aug | Sept | Oct | Nov | Dec | 1962 Jan | Feb | Mar | Apr | May | June |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chaetoceros* | .0594 | .1657 | .0654 | .0815 | .1022 | .1158 | .0973 | .1510 | .1733 | .1250 | .1812 | .5628 |
| *Rhizosolenia* | .0883 | .1237 | .0493 | .3138 | .4617 | .0558 | .1616 | .0641 | .0743 | .0425 | .0233 | .2396 |
| *Skeletonema* | .1620 | .1201 | .0003 | .0023 | .0058 | .0124 | .0119 | .1604 | .0274 | .0016 | .0025 | .0331 |
| *Cyclotella* | .0264 | .1072 | .0954 | .0346 | .0244 | .0408 | .0104 | .0136 | .0109 | .0057 | .0195 | .0204 |
| *Thalassiothrix* | .0091 | .0362 | .0016 | .0735 | .0659 | .0312 | .0740 | .0205 | .0021 | .0035 | .0109 | .0210 |
| *Coscinodiscus* | .0301 | .0173 | .0155 | .0148 | .0385 | .0238 | .0061 | .0070 | .0129 | .0087 | .0072 | .0087 |
| *Bacteriastrum* | .0100 | .0063 | 0 | .0034 | .0100 | .0301 | .0022 | 0 | 0 | .0012 | .0028 | .1153 |
| *Thalassionema* | .0043 | .0043 | .0058 | .0134 | .0053 | .0069 | .0072 | .0062 | .0024 | .0024 | .0024 | .0019 |
| Rest | .1177 | .0586 | .0758 | .0594 | .1241 | .0991 | .0412 | .0396 | .1182 | .0330 | .0745 | .1065 |
| Total volume ($mm^3/l$) | .5073 | .6401 | .2436 | .5966 | .8378 | .4157 | .4119 | .4624 | .4215 | .2237 | .3243 | 1.1092 |
| Total # ($10^6$ cells/l) | .487 | 1.436 | .844 | .687 | .436 | .617 | .551 | 1.199 | .822 | .635 | .957 | .902 |
| Types of diatoms | 21 | 24 | 14 | 17 | 25 | 25 | 19 | 18 | 26 | 18 | 17 | 25 |
| Chlorophyll *a* ($mg/m^3$) | 4.18 | 3.21 | 2.10 | .52 | 2.52 | 2.79 | 1.28 | 1.14 | 1.26 | 2.15 | 2.27 | 2.29 |
| Surface temp (C) | 28.8 | 28.8 | 28.1 | 25.3 | 21.4 | 19.6 | 10.9 | 17.2 | 18.2 | 22.2 | 27.1 | 27.9 |

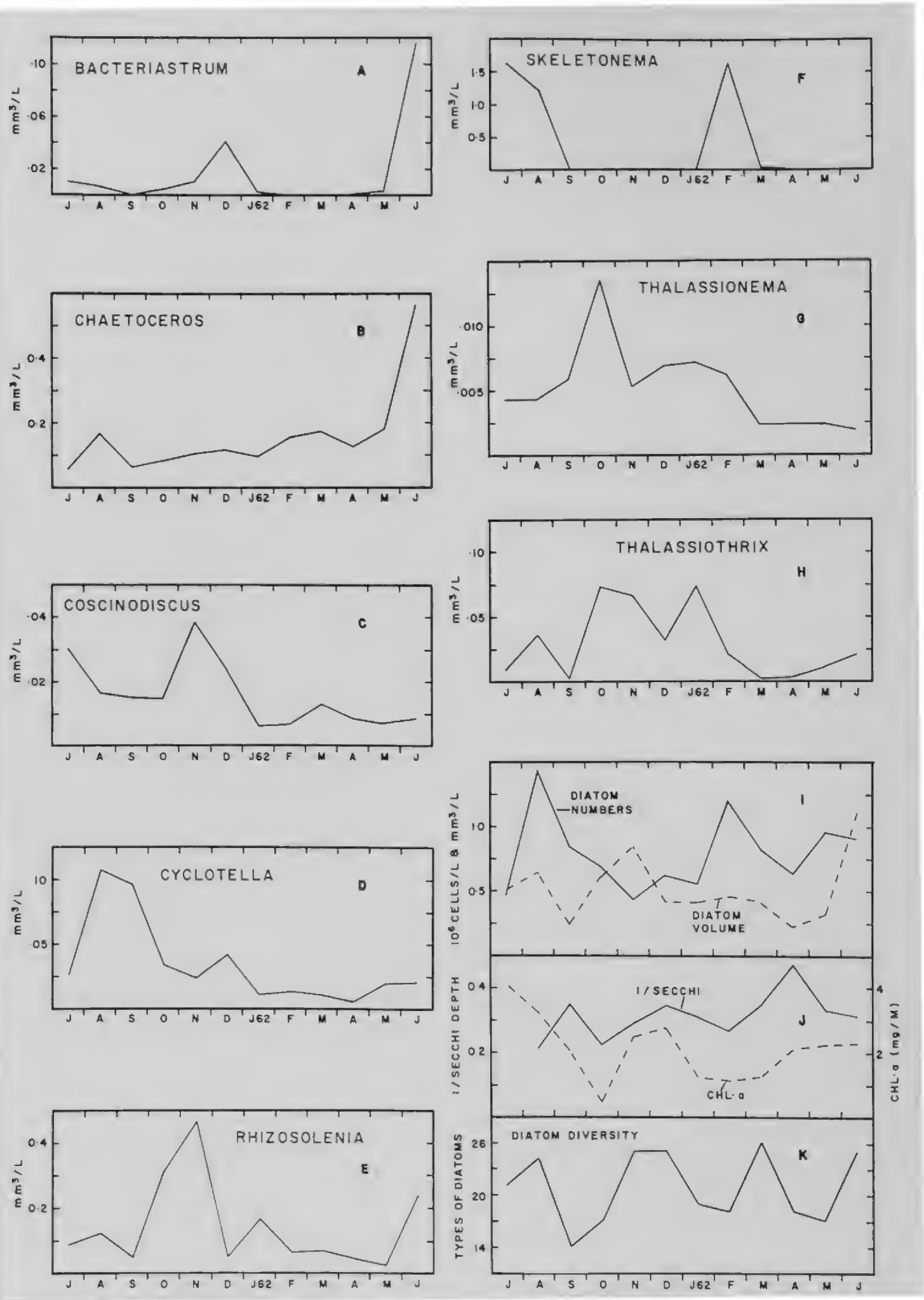


FIG. 3. Seasonal distribution of diatoms and chlorophyll-a in the St. Andrew Bay System in 1961–62. A—*Bacteriastrum*; B—*Chaetoceros*; C—*Coscinodiscus*; D—*Cyclotella*; E—*Rhizosolenia*; F—*Skeletonema*; G—*Thalassionema*; H—*Thalassiothrix*; I—Total diatom numbers and volume; J—Chlorophyll-a and 1/Secchi depth; K—Diatom variety.

## Zooplankton Distribution by Season and Station

### Species Account

The following account summarizes count and biomass data for individual species and types of zooplankton. Numerical and biomass contributions of each species of zooplankton by month are presented in Tables 8 and 9 and graphs of the seasonal biomass distribution of the major species in each plankton group are in Fig. 4 A–G. Tables 10 and 11 contain species count and biomass data according to salinity and station.

**Dinoflagellates:** The dinoflagellate *Noctiluca scintillans* (Macartney) is considered with zooplankton since it is holozoic in its mode of nutrition (Kofoid and Swezy, 1921). *Noctiluca* (Fig. 4 A) occurred first in 1961–62 in February and reached peak numbers (22,900/$m^3$) in March. This organism became well distributed throughout the bay complex, though it was more abundant in North and West Bays than in the eastern arm of the complex. After March *Noctiluca* all but disappeared and only small numbers occurred in aliquots of samples taken from April–June 1962. In 1959–60 a few *Noctiluca* were recorded as early as November and it was still present in February, though not nearly in such numbers as in February of 1962. In 1961–62 *Noctiluca* averaged 6.9% of the total zooplankton number and 2.4% of the total biomass.

**Tintinnids:** Thirteen species of tintinnids were identified from aliquots of zooplankton collections. According to Borror's (1962) literature survey this is the first list of species from the Gulf of Mexico. On the basis of two years of sampling there is evidence for seasonal changes in relative abundance of various species in this group. Species found predominantly in cooler months were *Favella taraikaensis* Hada, *Tintinnopsis kofoidi* Hada, *Helicostomella subulata* (Ehrenberg), *Codonellopsis obesa* Balech, and *Tintinnidium mucicola* (Claparède and Lachmann). The most abundant winter form was *Tintinnidium mucicola,* though *Tintinnopsis kofoidi, Favella taraikaensis* and *Heli costomella subulata* were also numerous. Species more common in the warmer months were *Favella panamensis* Kofoid and Campbell, *Tintinnopsis radix* (Imhof[a]), *Tintinnopsis brandti* (Nordqvist), *Amphorides amphora* (Claparède and Lachmann), *Eutintinnus medius* Kofoid and Campbell, and *Eutintinnus pinguis* Kofoid and Campbell. The most prevalent tintinnid of the warmer months was *Tintinnopsis radix* with *Favella panamensis* and *Tintinnopsis brandti* being abundant on occasion. Seasonal fluctuations of *Stylicauda platensis* (Da Cunha and Fonseca) and *Tintinnopsis buetschlii* Daday were not apparent.

Tintinnids were found in every survey and noticeable peaks of total numbers occurred in January and June of 1962. They also were encountered at every station and, like *Noctiluca,* they were generally more abundant in West and North Bays than in East Bay. This group made up 4.3% of the total number of zooplankters but because of their diminutive size only constituted 0.11% of the zooplankton biomass. Since these plankters easily could have passed through the nets used in this survey, possibly only a small fraction of the tintinnid biomass was accounted for. Sampling the St. Andrew Bay System with a finer mesh net undoubtedly would disclose many additional species.

**Hydromedusae:** Hydromedusae were one of the more diverse groups (26 spp.) of the St. Andrew Bay plankton, though they made a comparatively insignificant contribu-

[a] *T. radix, T. kofoidi,* and *S. platensis* were not accurately separated in initial counts, but after re-examining many samples it is reasonably safe to state that *T. radix* was more prevalent in the warmer months and that *T. kofoidi* was essentially a winter form.

TABLE 8

Seasonal numerical distribution of zooplankton in the St. Andrew Bay System (average of all stations)
+ indicates observed in sample but not in aliquot

| | Aug. 59 | Nov. | Feb. 60 | June | July 61 | Aug. | Sep. | Oct. | Nov. | Dec. | Jan. 62 | Feb. | Mar. | April | May | June |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DINOFLAGELLATA | | | | | | | | | | | | | | | | |
| Noctiluca scintillans | .... | 9 | 4 | .... | .... | .... | .... | .... | .... | .... | .... | 10553 | 22882 | 6 | 2 | 2 |
| TINTINNOINEA | | | | | | | | | | | | | | | | |
| Tintinnopsis radix | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Stylicauda platensis | 903 | 338 | 4 | 750 | + | 674 | 934 | 354 | 57 | 42 | 2547 | 24 | 603 | 154 | 57 | 13238 |
| Tintinnopsis kofoidi | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Tintinnopsis beutschlii | .... | .... | + | + | .... | .... | + | .... | .... | .... | 95 | + | 101 | .... | .... | 323 |
| Tintinnopsis brandti | 41 | 14 | .... | .... | .... | 489 | 43 | .... | .... | .... | .... | .... | 6 | .... | 5 | 833 |
| Tintinnidium mucicola | .... | .... | 13 | .... | .... | .... | .... | .... | .... | .... | 7647 | .... | + | + | .... | 140 |
| Eutintinnus medius | .... | .... | .... | + | .... | .... | .... | .... | + | .... | .... | .... | .... | .... | + | 123 |
| Eutintinnus pinguis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | + |
| Codonellopsis obesa | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 329 | .... | .... | .... | .... | .... |
| Helicostomella subulata | .... | + | + | .... | .... | .... | .... | .... | .... | .... | 991 | + | 33 | .... | .... | .... |
| Amphorides amphora | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | + |
| Favella panamensis | 2 | .... | .... | 69 | + | + | + | + | + | + | .... | .... | .... | .... | 8 | 1652 |
| Favella taraikaensis | .... | .... | 43 | .... | .... | .... | .... | .... | .... | .... | 1790 | .... | + | + | .... | .... |
| HYDROMEDUSAE | | | | | | | | | | | | | | | | |
| Aglaura hemistoma | .... | 2 | .... | .... | .... | 2 | 1 | .... | 1 | .... | .... | .... | .... | .... | .... | .... |
| Bougainvillia carolinensis | 1 | + | 1 | .... | .... | .... | 8 | .... | .... | 1 | + | 1 | + | 1 | .... | 2 |
| Cunina octonaria | 1 | + | .... | + | .... | + | 5 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Dipurena ophiogaster | .... | .... | 1 | .... | 1 | 1 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Dipurena strangulata | 1 | .... | .... | .... | 1 | .... | .... | + | + | .... | .... | .... | .... | .... | + | 8 |
| Ectopleura dumortieri | .... | .... | 1 | .... | .... | .... | + | .... | + | .... | 3 | .... | 1 | .... | 1 | + |
| Eirene pyramidalis | + | + | .... | .... | .... | .... | + | + | .... | .... | .... | .... | .... | .... | .... | .... |
| Eucheilota duodecimalis | 11 | 2 | 10 | 5 | 2 | 11 | 38 | 15 | 3 | 1 | 2 | + | 1 | 1 | 55 | 15 |
| Eucheilota ventricularis | + | .... | .... | + | .... | 1 | + | .... | .... | .... | .... | .... | .... | .... | 1 | + |
| Euphysa aurata | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 1 | 2 | + | .... |
| Euphysora gracilis | + | + | 1 | + | .... | .... | .... | .... | 1 | .... | .... | .... | .... | .... | + | 1 |
| Eutima variabilis | + | .... | .... | + | .... | 1 | + | .... | .... | .... | .... | .... | .... | .... | 1 | + |
| Halitiara formosa | + | + | .... | .... | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Liriope tetraphylla | 4 | + | 1 | 13 | 1 | 19 | 45 | 3 | 1 | 6 | 3 | 2 | 1 | 1 | 9 | 29 |
| Nemopsis bachei | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Obelia spp. | 1 | 2 | + | .... | 2 | 2 | 1 | .... | .... | .... | .... | + | .... | .... | + | 1 |
| Persa incolorata | .... | 1 | 22 | .... | .... | .... | .... | 3 | 2 | 7 | 8 | 1 | 1 | 7 | + | + |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phialidium folleatum | 8 | | | 18 | 3 | 10 | 24 | 7 | 3 | 1 | | | | | 41 | 17 |
| Phialucium carolinae | | | | | | | + | | | | | | | | | |
| Podocoryne minima | | | 1 | + | 1 | + | 1 | 84 | 145 | 16 | + | 1 | . | 1 | + | 46 |
| Podocoryne minuta | | | | | | 1 | 7 | 1 | | | | | | | | |
| Poboscidactyla ornata | + | | + | + | | | | + | | | 2 | + | | + | + | 1 |
| Rhopalonema velatum | | | | | | 1 | | | | | | | | | | |
| Sarsia sp. | | | | | | | | | 2 | | | | | | 1 | |
| Solmaris sp. | | | | + | | | | | | | | | | | 1 | |
| SIPHONOPHORA | | | | | | | | | | | | | | | | |
| Agalma sp. | + | | + | | | + | + | | | | + | | | | | + |
| Bassia bassensis | | | | | | | | | | | | | | | | + |
| Diphyes dispar | + | | + | | + | | | | | | | + | | | | |
| Enneagonum hyalinum | | | | | | | | | | | | + | | | | |
| Muggiaea kochi | 18 | | 4 | + | + | 2 | 1 | 2 | 2 | 1 | 1 | + | 1 | + | 2 | 2 |
| ROTIFERA | | | | | | | | | | | | | | | | |
| Synchaeta sp. | | 227 | 35 | | | | | | 261 | 3280 | 19260 | 12 | 7 | 8 | 69 | |
| Trichocerca marina | | 27 | 5 | | | | | 5 | | | 198 | | | | 47 | 780 |
| Rotifer C | | | | | | | | | 7 | | 94 | | | | 38 | |
| MOLLUSCA | | | | | | | | | | | | | | | | |
| Creseis acicula | 17 | | | 69 | 21 | 10 | 5 | 15 | 2 | 6 | 3 | | 1 | 411 | 23 | 7 |
| Desmopterus papilio | | | | | | + | | | | | | | | | | |
| Pteropod A | | | | + | | + | + | | | | | | | | | |
| Protatlanta souleyeti | | | + | + | | + | | | | | | | | | | + |
| POLYCHAETA | | | | | | | | | | | | | | | | |
| Tomopteris mariana | | | | | | | + | + | | | | | | | 2 | + |
| COPEPODA | | | | | | | | | | | | | | | | |
| Acartia tonsa | 2487 | 5132 | 4994 | 2676 | 4349 | 5387 | 8162 | 7326 | 4114 | 3364 | 9138 | 1330 | 2049 | 2565 | 9989 | 4289 |
| Anomalocera ornata | | | | | | | | | | 2 | | | | | | |
| Calanopia americana | 5 | | | | | 3 | 14 | 6 | 8 | | | | | | | |
| Candacia sp. (immatures) | | | | | | | | | | | 3 | | | | | |
| Centropages furcatus | 158 | 40 | | 114 | 69 | 225 | 535 | 247 | 60 | 20 | 2 | | 3 | 13 | 302 | 199 |
| Centropages hamatus | | 6 | 439 | | | | | | 20 | 106 | 1382 | 56 | 736 | 77 | | |
| Clausocalanus furcatus | | | | | 42 | 3 | | 48 | | | | | 2 | 5 | | |
| Clytemnestra rostrata | | | | 3 | | | | 3 | 8 | | | | | 2 | | |
| Corycaeus americanus | 12 | 8 | 12 | 13 | 20 | 15 | 11 | 11 | 14 | 13 | 13 | 3 | 68 | 21 | 70 | 81 |
| Corycaeus amazonicus | 12 | | 4 | 49 | | 10 | 7 | 18 | 6 | 3 | | | 2 | 10 | 5 | 40 |

TABLE 8 (Continued)

Seasonal numerical distribution of zooplankton in the St. Andrew Bay System (average of all stations)
+ indicates observed in sample but not in aliquot

| | Aug. 59 | Nov. | Feb. 60 | June | July 61 | Aug. | Sep. | Oct. | Nov. | Dec. | Jan. 62 | Feb. | Mar. | April | May | June |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Corycaeus giesbrechti | 5 | 8 | .... | 5 | .... | 3 | .... | 21 | 6 | 3 | .... | .... | .... | .... | .... | 2 |
| Corycaeus latus | .... | .... | .... | .... | .... | .... | .... | 5 | .... | .... | .... | .... | .... | .... | .... | .... |
| Corycaeus speciosus | .... | .... | .... | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Corycaeus spp. (immatures) | 33 | 50 | .... | 56 | 132 | 146 | 140 | 44 | 109 | 65 | 21 | 30 | 24 | 163 | 172 | 135 |
| Corycella carinata | .... | .... | .... | .... | .... | .... | 4 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eucalanus pileatus | 26 | 6 | 20 | 3 | 30 | 13 | 62 | 20 | 13 | 5 | 12 | 3 | 5 | 5 | 59 | 28 |
| Euterpina acutifrons | 81 | 49 | 120 | 889 | 91 | 203 | 352 | 114 | 241 | 38 | 176 | 22 | 216 | 256 | 1114 | 340 |
| Harpacticoids (benthic) | 9 | 4 | 3 | 10 | 13 | 38 | 24 | 21 | 27 | 33 | 16 | 9 | 76 | 30 | 100 | 88 |
| Hemicyclops type immatures | 48 | 95 | 17 | 3 | 85 | 36 | 44 | 48 | 24 | 24 | 42 | 20 | 4 | 20 | 27 | 173 |
| Kelleria sp. | 54 | 13 | 4 | 13 | .... | .... | 15 | .... | 20 | .... | 7 | 2 | .... | .... | 4 | 119 |
| Labidocera aestiva | 34 | .... | 8 | 108 | 124 | 65 | 86 | 121 | 177 | 25 | 22 | 6 | 39 | 5 | 66 | 110 |
| Microsetella norvegica | .... | .... | .... | 3 | .... | 17 | 4 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Oithona brevicornis | 944 | 2456 | 3896 | 6880 | 3544 | 10026 | 5548 | 5842 | 3755 | 3969 | 3794 | 785 | 2158 | 2020 | 2127 | 6633 |
| Oithona nana | 278 | 197 | 261 | 925 | 303 | 1528 | 1167 | 913 | 1283 | 248 | 547 | 146 | 1421 | 127 | 1968 | 1282 |
| Oithona plumifera | .... | 8 | 40 | .... | .... | 27 | .... | 5 | 4 | .... | 3 | .... | .... | .... | 2 | .... |
| Oithona simplex | 57 | 7 | 10 | .... | 46 | 320 | 378 | 794 | 935 | 70 | 46 | .... | 2 | .... | .... | 4 |
| Oncaea curta | 16 | 161 | 12 | 189 | 96 | 192 | 23 | 25 | 380 | 183 | 24 | 9 | 25 | 15 | 57 | 23 |
| Oncaea venusta | .... | 8 | .... | 6 | 2 | 30 | .... | .... | 4 | .... | .... | .... | 2 | .... | 2 | .... |
| Paracalanus aculeatus | .... | .... | 4 | .... | .... | .... | .... | .... | 4 | .... | 3 | .... | .... | .... | .... | .... |
| Paracalanus crassirostris | 1813 | 4805 | 1216 | 10789 | 6910 | 15575 | 8936 | 8199 | 5254 | 2798 | 2046 | 266 | 1489 | 834 | 4069 | 20976 |
| Paracalanus parvus | 140 | 51 | 146 | 305 | 159 | 178 | 108 | 214 | 639 | 93 | 175 | 28 | 181 | 300 | 753 | 179 |
| Pseudodiaptomus coronatus | 79 | 70 | 16 | 48 | 24 | 84 | 458 | 233 | 277 | 73 | 146 | 10 | 8 | 39 | 171 | 50 |
| Temora stylifera | .... | .... | .... | .... | 2 | .... | .... | 2 | .... | .... | 2 | .... | .... | .... | .... | .... |
| Temora turbinata | 84 | 126 | .... | 2 | 4 | 10 | 348 | 46 | 156 | 22 | 31 | 2 | 5 | 2 | 52 | 7 |
| Tortanus setacaudatus | 4 | 13 | .... | 17 | 65 | 59 | 52 | 47 | 4 | 2 | .... | .... | .... | .... | 4 | 14 |
| Undinula vulgaris | .... | .... | .... | .... | .... | + | .... | 10 | 2 | .... | .... | .... | .... | .... | .... | .... |
| Copepod nauplii | 1054 | 7884 | 1626 | 4745 | 1944 | 6767 | 5094 | 5432 | 7189 | 2130 | 4727 | 719 | 2541 | 1603 | 7141 | 17909 |
| CLADOCERA | | | | | | | | | | | | | | | | |
| Evadne tergestina | 408 | 46 | .... | 768 | 649 | 2090 | 630 | 382 | 131 | 11 | .... | .... | .... | .... | 368 | 126 |
| Penilia avirostris | 19 | 2 | .... | 72 | 11 | 121 | 241 | 89 | 88 | 9 | .... | .... | .... | .... | 67 | 82 |
| Podon polyphemoides | .... | .... | 340 | + | .... | .... | 1 | .... | 2 | 81 | 1812 | 120 | 887 | 289 | 361 | .... |
| OSTRACODA | | | | | | | | | | | | | | | | |
| Euconchoecia chierchiae | .... | 2 | 133 | .... | 40 | 49 | 1 | 4 | 22 | 28 | 7 | 1 | .... | .... | .... | .... |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AMPHIPODA | | | | | | | | | | | | | | | | |
| Hyperia atlantica | 1 | + | 8 | 2 | 6 | 1 | .... | + | 1 | .... | 1 | .... | + | .... | 1 | 2 |
| Simorhynchotus antennarius | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | + |
| MYSIDACEA | | | | | | | | | | | | | | | | |
| Gastrosaccus dissimilis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | + |
| Metamysidopsis munda | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 1 | .... | .... | .... | .... | .... |
| Mysidopsis almyra | .... | .... | .... | .... | .... | .... | .... | .... | .... | + | .... | .... | .... | .... | .... | .... |
| DECAPODA | | | | | | | | | | | | | | | | |
| Lucifer faxoni | 9 | + | .... | 5 | 6 | 6 | 24 | 20 | 4 | 1 | .... | + | 1 | .... | 5 | 63 |
| CHAETOGNATHA | | | | | | | | | | | | | | | | |
| Sagitta enflata | 5 | 19 | 3 | 5 | 1 | 6 | 1 | 3 | 3 | 2 | 5 | .... | .... | .... | .... | .... |
| Sagitta helenae | 2 | .... | .... | 1 | 1 | 1 | .... | .... | .... | 1 | .... | + | 1 | .... | 5 | 63 |
| Sagitta hispida | 7 | 2 | 8 | 3 | 6 | .... | 9 | 8 | 1 | .... | .... | .... | .... | .... | 2 | .... |
| Sagitta tenuis | 28 | 5 | 8 | 29 | 7 | 9 | 19 | 21 | 18 | 7 | 10 | .... | 14 | 4 | 49 | 64 |
| Sagitta < 3 mm | 119 | 128 | 24 | 143 | 177 | 250 | 117 | 226 | 120 | 51 | 40 | 25 | 26 | 67 | 249 | 508 |
| APPENDICULARIA | | | | | | | | | | | | | | | | |
| Appendicularia sicula | .... | .... | .... | 1012 | 17 | 24 | .... | .... | .... | 7 | 5 | 4 | .... | 12 | 20 | .... |
| Fritillaria borealis | .... | .... | .... | .... | 12 | .... | .... | .... | .... | .... | .... | .... | .... | .... | 19 | 9 |
| Fritillaria formica | .... | 11 | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Fritillaria haplostoma | .... | 10 | .... | .... | .... | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... |
| Oikopleura dioica | 889 | 889 | 116 | 1770 | 1435 | 4688 | 3786 | 3156 | 3750 | 334 | 105 | 41 | 1383 | 1473 | 5326 | 4482 |
| Oikopleura cornutogastra | .... | .... | .... | .... | .... | .... | .... | 11 | .... | .... | .... | .... | .... | .... | .... | .... |
| Oikopleura fusiformis | 31 | 47 | 6 | + | 74 | 179 | 52 | 243 | 75 | + | 1 | 2 | 72 | 458 | 41 | 14 |
| Oikopleura longicauda | 651 | 34 | 46 | 609 | 86 | 1640 | 521 | 235 | 103 | 7 | 80 | 14 | 77 | 192 | 358 | 445 |
| Oikopleura rufescens | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | + | .... |
| Kowalevskaia tenuis | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| THALIACEA | | | | | | | | | | | | | | | | |
| Cyclosalpa floridana | .... | .... | .... | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Dolioletta gegenbauri | 5 | .... | .... | + | 1 | 4 | 6 | 3 | 1 | + | 4 | 5 | .... | .... | 21 | 14 |
| LARVAE | | | | | | | | | | | | | | | | |
| Polychaete | 155 | 153 | 143 | 269 | 141 | 373 | 288 | 450 | 355 | 507 | 836 | 80 | 410 | 311 | 1352 | 4283 |
| Gastropod | 619 | 58 | 338 | 725 | 979 | 2425 | 4072 | 553 | 384 | 66 | 93 | 17 | 209 | 143 | 1727 | 2816 |
| Pelecypod | 217 | 76 | 493 | 1955 | 596 | 2501 | 2485 | 759 | 1301 | 427 | 209 | 39 | 1078 | 868 | 2164 | 4335 |
| Cirriped | 29 | 56 | 586 | 186 | 151 | 60 | 61 | 166 | 406 | 330 | 162 | 98 | 323 | 179 | 303 | 441 |
| Decapod | 189 | .... | .... | 66 | 90 | 232 | 376 | 141 | 54 | 13 | 2 | 2 | 31 | 14 | 154 | 376 |
| Echinoderm | 51 | 4 | 19 | 58 | 24 | 191 | 161 | 74 | 16 | 13 | 22 | .... | 67 | 173 | 217 | 9171 |
| Other invertebrate | 34 | 55 | 54 | 32 | 8 | 24 | 60 | 24 | 85 | 88 | 69 | 25 | 88 | 44 | 125 | 166 |
| Cephalochordate | 1 | .... | .... | 1 | 2 | .... | 4 | 1 | .... | .... | .... | .... | .... | 12 | .... | 8 |
| Fish eggs | 22 | .... | .... | 18 | 5 | 66 | 4 | 9 | .... | 9 | .... | .... | 3 | .... | 95 | 41 |
| Fish larvae | 17 | .... | .... | 18 | 13 | 21 | 10 | .... | 1 | .... | .... | .... | .... | 3 | 16 | 32 |

TABLE 9

Seasonal dry weight ($mg/m^3$) distribution of zooplankton in the St. Andrew Bay System (average of all stations)

| | Aug. 59 | Nov. | Feb. 60 | June | July 61 | Aug. | Sep. | Oct. | Nov. | Dec. | Jan. 62 | Feb. | Mar. | April | May | June |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DINOFLAGELLATA | | | | | | | | | | | | | | | | |
| Noctiluca scintillans | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 3.91 | 8.47 | .... | .... | .... |
| TINTINNOINEA | | | | | | | | | | | | | | | | |
| Tintinnopsis radix | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Stylicauda platensis | .... | .... | .... | .... | .... | .01 | .01 | .... | 0.1 | .... | .03 | .... | .01 | .... | .... | .16 |
| Tintinnopsis kofoidi | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Tintinnopsis beutschlii | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Tintinnopsis brandti | .... | .... | .... | .... | .... | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .02 |
| Tintinnidium mucicola | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .16 | .... | .... | .... | .... | .... |
| Eutintinnus medius | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eutintinnus pinguis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Codonellopsis obesa | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .01 | .... | .... | .... | .... | .... |
| Helicostomella subulata | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Amphorides amphora | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Favella panamensis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .20 |
| Favella taraikaensis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .09 | .... | .... | .... | . | .... |
| HYDROMEDUSAE | | | | | | | | | | | | | | | | |
| Aglaura hemistoma | .. | .. | .... | .... | .... | .... | .01 | .... | .01 | .. | .... | | . | .... | .... | .... |
| Bougainvillia carolinensis | .... | .... | .... | .... | .... | .... | .10 | .... | .... | .... | .... | .... | .... | .... | .... | .03 |
| Cunina octonaria | .... | .... | .... | .... | .... | .... | .14 | .... | .... | .. | .... | .... | .. | .... | .. | .. |
| Dipurena ophiogaster | .... | .... | .... | .... | .... | .01 | .... | .... | .. | .... | .... | .... | .... | .... | .... | . |
| Dipurena strangulata | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .03 |
| Ectopleura dumortieri | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eirene pyramidalis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .01 | .... | .... | .... | .... | .... | .... |
| Eucheilota duodecimalis | .... | .... | .... | .... | .02 | .03 | .12 | .04 | .01 | .... | .02 | .... | .... | .... | .16 | .04 |
| Eucheilota ventricularis | .... | .... | .... | .... | .... | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .06 | .... |
| Euphysa aurata | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Euphysora gracilis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eutima variabilis | .... | .... | .... | .... | .... | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .06 | .... |
| Halitiara formosa | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Liriope tetraphylla | .. | .... | .... | .... | .02 | .05 | .46 | .07 | .01 | .03 | .... | .01 | .. | .. | .04 | .46 |
| Nemopsis bachei | .... | .... | .... | .... | .... | .... | .. | . | .. | .... | .... | .... | .... | .. | .... | .. |
| Obelia spp. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Persa incolorata | .... | .... | .... | .... | .... | .... | .... | .01 | .... | .02 | .03 | .... | .... | .01 | . | .... |
| Phialidium folleatum | .... | .... | .... | .... | .05 | .08 | .16 | .02 | .02 | .... | .... | .... | .... | .... | .38 | .22 |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phialucium carolinae | .... | .... | .... | .... | .... | .... | .... | .... | .... | .. | .... | .... | .... | .... | .... | .... |
| Podocoryne minima | .... | .... | .... | .... | .... | .... | .. | .13 | .22 | .02 | .... | .... | .... | .... | .... | .06 |
| Podocoryne minuta | .... | .... | .... | .... | .... | .... | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Proboscidactyla ornata | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .04 | .... | .... | .... | .... | .01 |
| Rhopalonema velatum | .... | .... | .... | .... | .... | .03 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Sarsia sp. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Solmaris sp. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .. | .... | .... | .... | .... | .... | .... |
| SIPHONOPHORA | | | | | | | | | | | | | | | | |
| Agalma sp. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .. | .. | .... | .... | .... | ... | .. |
| Bassia bassensis | .... | .... | .... | .. | .... | .. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Diphyes dispar | .... | .. | .... | .... | .... | .... | .... | .... | .. | .. | .. | .... | .... | .... | .... | .... |
| Enneagonum hyalinum | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .. | .... | .... | .... | .... |
| Muggiaea kochi | .... | .. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| ROTIFERA | | | | | | | | | | | | | | | | |
| Synchaeta sp. | .... | .... | .... | .... | .. | .... | . | .. | .06 | .79 | 4.62 | .... | .... | .. | .02 | .... |
| Trichocerca marina | .... | .. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Rotifer C | .... | ... | .... | .... | .... | .... | .... | .. | .. | .... | .... | .. | .... | .... | .... | .... |
| MOLLUSCA | | | | | | | | | | | | | | | | |
| Creseis acicula | .... | .... | .... | .... | .03 | .01 | .01 | .02 | .... | .01 | .... | .... | .... | .52 | .03 | .05 |
| Desmopterus papilio | .... | .. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Pteropod A | .... | .... | .... | .... | .. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Protatlanta souleyeti | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| POLYCHAETA | | | | | | | | | | | | | | | | |
| Tomopteris mariana | .... | .... | .... | .. | .. | .... | .. | .... | .... | .... | .. | .... | .... | .. | .... | .... |
| COPEPODA | | | | | | | | | | | | | | | | |
| Acartia tonsa | .... | .... | .... | .. | 7.14 | 9.98 | 16.26 | 12.58 | 5.22 | 6.10 | 18.97 | 1.80 | 2.73 | 3.28 | 12.18 | 4.78 |
| Anomalocera ornata | .... | .... | .... | .... | .... | .. | .. | .. | .. | .01 | .. | .... | .... | .... | .... | .... |
| Calanopia americana | .... | .... | .... | .... | .. | .01 | .04 | .02 | .04 | .... | .... | .. | .... | .... | .... | .... |
| Candacia sp. (immatures) | .... | .... | .... | .... | .... | .... | .... | .... | .... | . | . | .... | .. | .. | .. | .. |
| Centropages furcatus | .... | .... | .. | .... | .21 | .77 | 1.27 | .64 | .23 | .03 | .. | .... | .01 | .07 | 1.19 | .43 |
| Centropages hamatus | .... | .... | .... | .... | .... | .... | .... | .. | .05 | .24 | 3.51 | .08 | 1.22 | .17 | .... | .... |
| Clausocalanus furcatus | .... | .... | .... | .... | .26 | .01 | .... | .09 | .. | .... | .... | .... | .02 | .06 | .... | .... |
| Clytemnestra rostrata | .... | .... | .... | .... | .. | .... | .... | . | .01 | .. | .... | .. | .... | .01 | .. | . |
| Corycaeus americanus | .... | .... | .... | .... | .01 | .06 | .04 | .03 | .05 | .05 | .05 | .01 | .30 | .10 | .23 | .27 |
| Corycaeus amazonicus | .... | .... | .... | .... | .... | .05 | .02 | .05 | .02 | .01 | .... | .. | .01 | .03 | .03 | .17 |
| Corycaeus giesbrechti | .... | .... | .... | .... | .... | .02 | .... | .07 | .01 | .01 | .... | .... | .... | .... | .... | .02 |
| Corycaeus latus | .... | .... | .... | .... | .. | .. | .... | .04 | .. | .. | .... | .. | .. | .... | .. | .... |

TABLE 9 (Continued)

Seasonal dry weight (mg/m³) distribution of zooplankton in the St. Andrew Bay System (average of all stations)

| | Aug. 59 | Nov. | Feb. 60 | June | July 61 | Aug. | Sep. | Oct. | Nov. | Dec. | Jan. 62 | Feb. | Mar. | April | May | June |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Corycaeus speciosus | .... | .... | .... | .... | ... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Corycaeus spp. (immatures) | .. | .... | .. | .. | .10 | .14 | .10 | .05 | .13 | .08 | .02 | .03 | .05 | .23 | .16 | .19 |
| Corycella carinata | .. | .. | . | .. | .... | .... | .01 | .. | .. | .. | .... | .... | .... | .... | .... | .... |
| Eucalanus pileatus | . | .... | .. | . | .23 | .40 | 1.18 | .15 | .20 | .09 | .05 | .01 | .14 | .12 | 1.37 | .39 |
| Euterpina acutifrons | .. | .... | .... | .. | .09 | .19 | .42 | .12 | .25 | .06 | .16 | .02 | .24 | .26 | 1.53 | .48 |
| Harpacticoids (benthic) | .... | .... | .... | .... | .01 | .03 | .02 | .02 | .02 | .03 | .02 | .01 | .08 | .03 | .10 | .07 |
| Hemicyclops type immatures | .... | .... | ... | ... | .07 | .03 | .05 | .05 | .02 | .02 | .06 | .02 | .01 | .02 | .02 | .13 |
| Kelleria sp. | .... | .. | .. | .. | .. | .... | .03 | ... | .05 | ... | .. | ... | . | .... | .. | .27 |
| Labidocera aestiva | .... | .. | .... | .. | .41 | .24 | .18 | .53 | .65 | .07 | .04 | .01 | .07 | .01 | .14 | .34 |
| Microsetella norvegica | .... | .... | .... | .. | .... | .01 | ... | .... | .... | .. | .... | .... | .... | .. | .. | .... |
| Oithona brevicornis | .... | .... | .... | .... | 2.66 | 6.30 | 4.25 | 4.90 | 2.98 | 3.91 | 3.43 | .73 | 1.87 | 1.83 | 1.78 | 4.72 |
| Oithona nana | .... | .... | .... | .. | .22 | 1.14 | .97 | .65 | 1.46 | .28 | .48 | .13 | 1.40 | .11 | 1.68 | .98 |
| Oithona plumifera | .... | .... | .... | .... | .... | .04 | .... | .... | .01 | .. | .. | .... | .... | .... | . | .... |
| Oithona simplex | .. | .. | .. | .... | .04 | .24 | .28 | .59 | .73 | .06 | .04 | ... | ... | .... | ... | .... |
| Oncaea curta | .... | .. | .. | .. | .07 | .16 | .02 | .02 | .36 | .20 | .02 | .01 | .02 | .02 | .05 | .02 |
| Oncaea venusta | .... | .... | .. | .... | .... | .07 | .... | .. | . | .. | .. | .... | .01 | .... | .01 | .... |
| Paracalanus aculeatus | .... | .... | .... | .... | .... | .... | .... | . | .04 | .... | .03 | .... | .... | .... | .... | .... |
| Paracalanus crassirostris | .... | .. | .. | .... | 6.36 | 12.45 | 7.97 | 7.49 | 5.68 | 3.09 | 2.05 | .27 | 2.06 | .93 | 3.80 | 12.29 |
| Paracalanus parvus | .. | .... | .. | .... | .27 | .25 | .15 | .41 | 2.17 | .23 | .23 | .03 | .40 | .83 | 1.71 | .35 |
| Pseudodiaptomus coronatus | .... | .... | .... | .... | .02 | .10 | .69 | .22 | .35 | .10 | .14 | .01 | .01 | .04 | .18 | .05 |
| Temora stylifera | .... | .... | .. | .... | .14 | .. | .... | .03 | .... | .... | .... | .... | .... | .. | .... | .... |
| Temora turbinata | .... | .... | .... | .. | .01 | .02 | .70 | .24 | .59 | .17 | .09 | .... | .01 | .... | .13 | .04 |
| Tortanus setacaudatus | .... | .... | .... | .... | .11 | .19 | .10 | .10 | .02 | .... | .. | .... | .... | .... | .... | .03 |
| Undinula vulgaris | .... | .... | .... | .... | .... | .... | .... | 1.59 | .... | .. | .... | .... | .... | .. | .... | .... |
| Copepod nauplii | .... | .. | .... | .. | 1.03 | 3.01 | 2.65 | 2.93 | 3.46 | 1.29 | 2.59 | .44 | 1.58 | .85 | 3.31 | 6.55 |
| CLADOCERA | | | | | | | | | | | | | | | | |
| Evadne tergestina | .... | .. | .. | .. | .79 | 2.51 | .76 | .46 | .16 | .01 | .. | .... | .... | .... | .44 | .15 |
| Penilia avirostris | .. | .. | .... | .... | .02 | .20 | .40 | .15 | .15 | .01 | .... | .... | .. | .... | .11 | .14 |
| Podon polyphemoides | . | .. | .... | .. | .. | .. | .. | .. | .. | .07 | 1.67 | .11 | .82 | .27 | .33 | .. |
| OSTRACODA | | | | | | | | | | | | | | | | |
| Euconchoecia chierchiae | .... | .... | .... | .. | .09 | .47 | .. | .01 | .05 | .08 | .01 | .... | .... | .... | .... | .... |
| AMPHIPODA | | | | | | | | | | | | | | | | |
| Hyperia atlantica | .... | .... | .... | .... | .16 | .02 | .... | .... | .04 | .... | .02 | .... | .... | .... | .01 | .05 |
| Simorhynchotus antennarius | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYSIDACEA | | | | | | | | | | | | | | | | |
| Gastrosaccus dissimilis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Metamysidopsis munda | .... | .... | .... | .... | .... | .... | .... | .... | .... | . .. | .... | . .. | .... | .... | . .. | .... |
| Mysidopsis almyra | .... | .... | .... | .... | .... | .... | . .. | .... | .... | .... | .. . | . | . . | .. | .... | .... |
| DECAPODA | | | | | | | | | | | | | | | | |
| Lucifer faxoni | .... | .... | . .. | . . | .07 | .30 | .35 | .24 | .04 | .01 | . | . | .02 | .... | .04 | .59 |
| CHAETOGNATHA | | | | | | | | | | | | | | | | |
| Sagitta enflata | .... | .... | . | . .. | .18 | .11 | .06 | .06 | .02 | .02 | .14 | | | . | | .21 |
| Sagitta helenae | .... | .... | . | ... | .01 | .01 | .. | . . | .... | . | | . .. | . .. | ... | .04 | .... |
| Sagitta hispida | .... | .... | .... | .... | .11 | . . | .18 | .18 | .03 | .04 | .20 | .01 | .19 | .... | .09 | .11 |
| Sagitta tenuis | .... | .... | ... | . .. | .12 | .15 | .27 | .29 | .28 | .09 | .22 | | .20 | .05 | .73 | .80 |
| Sagitta < 3mm | .... | .... | .... | .... | .22 | .64 | .20 | .30 | .15 | .08 | .06 | .04 | .05 | .08 | .68 | .69 |
| APPENDICULARIA | | | | | | | | | | | | | | | | |
| Appendicularia sicula | .... | .... | . .. | .... | .01 | .03 | . . | . . | .... | .01 | .01 | .... | .... | .01 | .01 | .... |
| Fritillaria borealis | .... | .... | .... | .... | .01 | .. . | .... | . . | .... | .. . | .... | .... | .... | .... | .05 | .02 |
| Fritillaria formica | .... | .. . | .... | .. . | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Fritillaria haplostoma | .. . | .... | .... | .... | ... | .... | .... | .... | .... | .... | .... | .. . | .. . | .... | .... | .... |
| Oikopleura dioica | .... | .... | . .. | .... | 1.40 | 6.25 | 5.42 | 4.15 | 5.14 | 4.99 | .20 | .05 | 2.65 | 1.89 | 6.40 | 3.53 |
| Oikopleura cornutogastra | .. | .... | .. . | .. | . | .... | .. . | .03 | .... | .... | .... | .... | .... | .... | .... | .... |
| Oikopleura fusiformis | | . .. | . .. | . .. | .08 | .24 | .10 | .47 | .12 | .... | .... | .... | .12 | .81 | .09 | .02 |
| Oikopleura longicauda | .... | .... | . . | .... | .09 | 1.79 | 1.04 | .36 | .18 | .01 | .20 | .02 | .15 | .35 | .62 | .43 |
| Oikopleura rufescens | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .03 | .... | .. . | .... |
| Kowalevskaia tenuis | . .. | .... | .... | .... | . .. | .. . | . .. | .... | . . | .... | .... | . . | .. . | .... | .... | .... |
| THALIACEA | | | | | | | | | | | | | | | | |
| Cyclosalpa floridana | .... | .... | . .. | | .... | .... | . .. | .... | .... | .... | .... | . | .... | .... | .... | .... |
| Dolioletta gegenbauri | .... | .... | . | .... | .02 | .02 | .05 | .02 | .01 | ... | .07 | .21 | . . | .... | .18 | .09 |
| LARVAE | | | | | | | | | | | | | | | | |
| Polychaete | .... | .... | . .. | .... | .52 | 1.38 | 1.07 | 1.67 | 1.31 | 1.88 | 3.09 | .30 | 1.52 | 1.15 | 5.00 | 15.85 |
| Gastropod | .. . | .... | . .. | .... | 2.60 | 6.45 | 10.83 | 1.39 | 1.02 | .18 | .25 | .04 | .56 | .38 | 4.59 | 7.49 |
| Pelecypod | . . | ... | ... | .. | 1.58 | 6.65 | 6.61 | 1.02 | 3.46 | 1.14 | .55 | .10 | 2.80 | 2.31 | 5.76 | 11.53 |
| Cirriped | .... | .... | .... | .... | .18 | .07 | .15 | .20 | .38 | .31 | .17 | .13 | .61 | .45 | .52 | .59 |
| Decapod | .... | .... | .... | .... | .49 | 1.26 | 2.04 | .76 | .29 | .07 | .01 | .01 | .17 | .08 | .84 | 2.04 |
| Echinoderm | .... | .... | .... | .... | .01 | .06 | .06 | .03 | . . | .... | .... | .... | .02 | .06 | .07 | 2.39 |
| Other invertebrate | .... | .... | .... | .... | .... | .... | .01 | .01 | .... | .... | .... | . . | .01 | . . | .04 | .. . |
| Cephalochordate | .... | .... | .... | .... | .01 | ... | .02 | .01 | .... | . . | .. . | .... | . | .05 | .. . | .03 |
| Fish eggs | .... | . . | .... | .... | .04 | .58 | .03 | .06 | . .. | .08 | .... | .... | .02 | .. . | .83 | .36 |
| Fish larvae | | . | .. . | .... | .08 | .14 | .06 | .... | .01 | .... | .... | .... | .... | .02 | .11 | .21 |

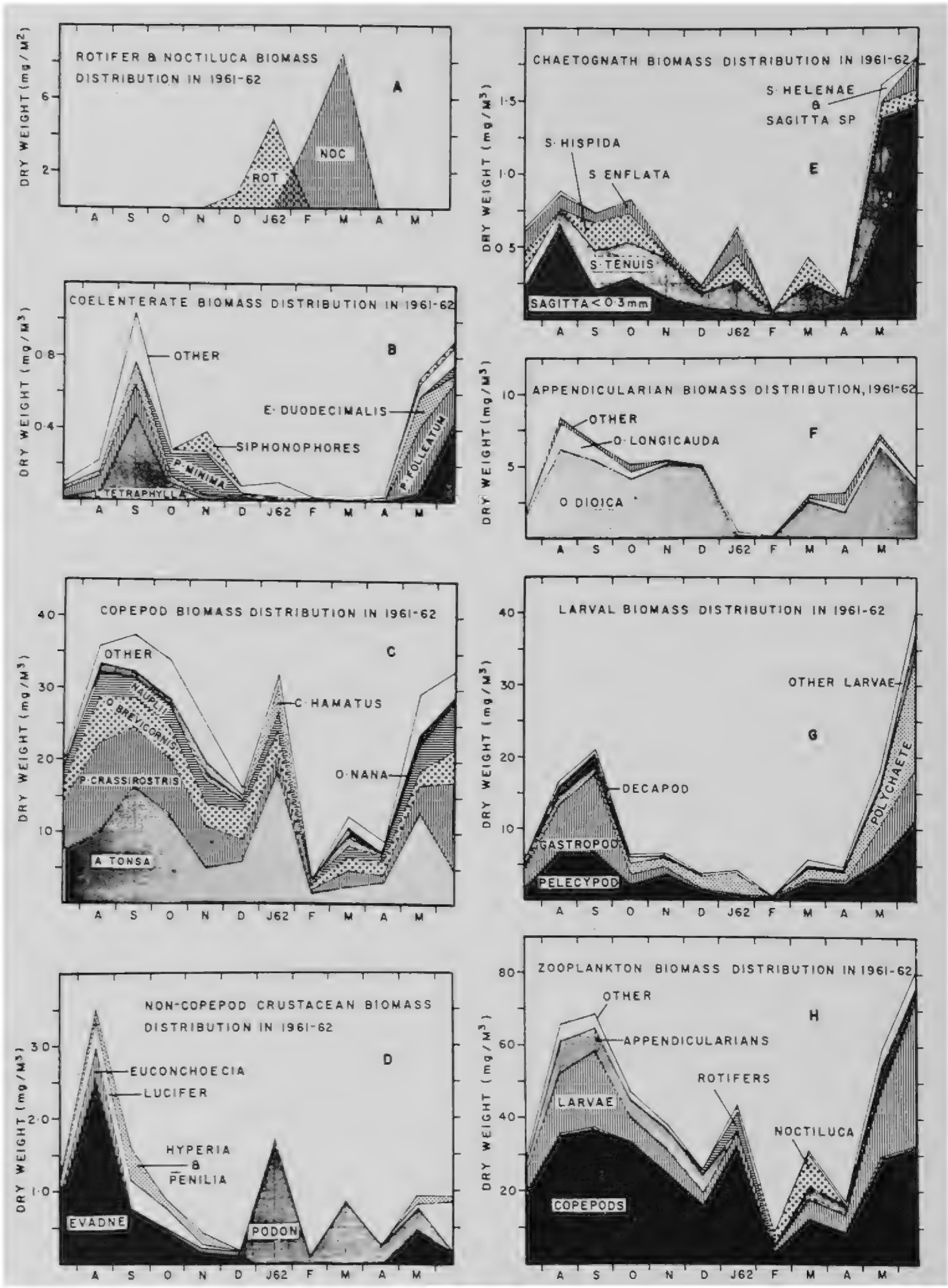


FIG. 4. Zooplankton distribution in the St. Andrew Bay System in 1961–62. A—Rotifers (*Synchaeta*) and *Noctiluca*; B—*Coelenterates*; C—Copepods; D—Non-copepod crustaceans; E—Chaetognaths; F—Appendicularians; G—Larvae; H—Total Zooplankton.

TABLE 10

Zooplankton numbers/m³ by station in the St. Andrew Bay System (1961–62 average values) Stations arranged in order of decreasing mean annual salinity + indicates observed in sample but not in aliquot

| | S3 | S2 | E4 | S1 | E3 | W2 | N2 | W1 | E2 | N1 | E1 | Avg. 1961–62 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DINOFLAGELLATA | | | | | | | | | | | | |
| Noctiluca scintillans | 4768 | 5486 | 877 | 3127 | 2515 | 6347 | 1638 | 2632 | 85 | 3209 | 20 | 2787 |
| TINTINNOINEA | | | | | | | | | | | | |
| Tintinnopsis radix | .... | .... | .... | .... | .... | .... | | | | | | |
| Stylicauda platensis | 207 | 521 | 1705 | 5605 | 1184 | 1286 | 3406 | 1237 | 1915 | 428 | 291 | 1557 |
| Tintinnopsis kofoidi | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Tintinnopsis beutschlii | .... | .... | 126 | 203 | 75 | 61 | 12 | .... | .... | .... | .... | 43 |
| Tintinnopsis brandti | .... | .... | + | .... | .... | 112 | 647 | 247 | 34 | 29 | 192 | 115 |
| Tintinnidium mucicola | .... | .... | 7 | 152 | 29 | 754 | 2172 | 974 | .... | 3050 | .... | 649 |
| Eutintinnus medius | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | 10 |
| Eutintinnus pinguis | .... | .... | 113 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Codonellopsis obesa | .... | .... | .... | .... | .... | 75 | 124 | .... | .... | 102 | .... | 27 |
| Helicostomella subulata | .... | .... | 13 | .... | .... | 17 | 124 | .... | .... | 610 | .... | 85 |
| Amphorides amphora | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Favella panamensis | .... | .... | 120 | .... | 243 | 27 | .... | .... | 1131 | .... | .... | 138 |
| Favella taraikaensis | .... | 83 | 28 | 76 | .... | 377 | 871 | 104 | .... | 102 | .... | .... |
| HYDROMEDUSAE | | | | | | | | | | | | |
| Aglaura hemistoma | 1 | 2 | + | .... | + | .... | .... | .... | .... | .... | .... | .... |
| Bougainvillia carolinensis | 3 | 2 | 3 | 1 | + | 1 | .... | .... | .... | .... | .... | 1 |
| Cunina octonaria | 3 | + | 1 | + | + | .... | .... | .... | .... | .... | .... | .... |
| Dipurena ophiogaster | .... | .... | .... | .... | .... | 1 | 1 | + | .... | .... | .... | .... |
| Dipurena strangulata | .... | 2 | 1 | + | + | .... | .... | 4 | + | .... | .... | 1 |
| Ectopleura dumortieri | 3 | + | + | 2 | + | .... | .... | .... | .... | .... | .... | .... |
| Eirene pyramidalis | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eucheilota duodecimalis | 15 | 10 | 23 | 6 | 24 | 14 | 12 | 11 | 9 | 2 | 5 | 12 |
| Eucheilota ventricularis | 1 | + | .... | .... | .... | + | .... | .... | .... | .... | .... | .... |
| Euphysa aurata | .... | + | + | 1 | + | .... | + | + | .... | .... | .... | .... |
| Euphysora gracilis | 1 | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eutima tariabilis | + | .... | + | .... | .... | .... | 1 | .... | 1 | .... | .... | .... |
| Halitiara formosa | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Liriope tetraphylla | 42 | 24 | 26 | 3 | 4 | 5 | 1 | 5 | 1 | .... | .... | 10 |
| Nemopsis bachei | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Obelia spp. | + | + | + | 1 | .... | 1 | .... | + | .... | 1 | 2 | 4 |
| Persa incolorata | 11 | 6 | 1 | 1 | + | + | + | .... | .... | .... | .... | 2 |

TABLE 10—Continued

Zooplankton numbers/m³ by station in the St. Andrew Bay System (1961–62 average values) Stations arranged in order of decreasing mean annual salinity + indicates observed in sample but not in aliquot

| | S3 | S2 | E4 | S1 | E3 | W2 | N2 | W1 | E2 | N1 | E1 | Avg. 1961–62 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phialidium folleatum | 10 | 8 | 21 | 15 | 10 | 5 | 12 | 3 | 5 | .... | 2 | 9 |
| Phialucium carolinae | .... | .... | + | + | + | .... | .... | .... | + | .... | .... | .... |
| Podocoryne minima | 2 | 3 | 32 | 4 | 53 | .... | 3 | 25 | 84 | 3 | 59 | 25 |
| Podocoryne minuta | 4 | 2 | 1 | + | 1 | .... | + | .... | .... | .... | + | 1 |
| Proboscidactyla ornata | 2 | + | + | + | .... | .... | .... | .... | .... | .... | .... | .... |
| Rhopalonema velatum | 1 | + | .... | + | .... | .... | .... | .... | .... | .... | .... | .... |
| Sarsia sp. | + | .... | .... | .... | 1 | + | + | .... | .... | .... | .... | .... |
| Solmaris sp. | 1 | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| SIPHONOPHORA | | | | | | | | | | | | |
| Agalma sp. | + | + | + | + | .... | .... | .... | .... | .... | .... | .... | .... |
| Bassia bassensis | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Diphyes dispar | + | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Enneagonum hyalinum | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 1 |
| Muggiaea kochi | 6 | 2 | 2 | 2 | .... | .... | + | .... | .... | .... | .... | 4 |
| ROTIFERA | | | | | | | | | | | | |
| Synchaeta sp. | .... | 17 | 188 | 129 | 3605 | 2139 | 1681 | 1579 | 3153 | 4109 | 4387 | 1908 |
| Trichocerca marina | .... | 15 | .... | 58 | 317 | 292 | 44 | 25 | 39 | 154 | .... | 86 |
| Rotifer C | .... | .... | 5 | .... | .... | 1 | 98 | 4 | .... | 19 | .... | 12 |
| MOLLUSCA | | | | | | | | | | | | |
| Creseis acicula | 402 | 54 | 2 | 1 | + | .... | .... | .... | + | .... | .... | 42 |
| Desmopterus papilio | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Pteropod A | 1 | + | 3 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Protatlanta souleyeti | + | + | + | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| POLYCHAETA | | | | | | | | | | | | |
| Tomopteris mariana | + | 1 | 5 | + | + | .... | .... | .... | .... | .... | .... | .... |
| COPEPODA | | | | | | | | | | | | |
| Acartia tonsa | 415 | 1520 | 4276 | 3590 | 5433 | 5823 | 6317 | 9350 | 8525 | 3489 | 8142 | 5172 |
| Anomalocera ornata | .... | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... |
| Calanopia americana | 16 | 3 | 2 | 3 | 2 | .... | .... | .... | 3 | .... | .... | 3 |
| Candacia sp. (immatures) | 3 | .... | 2 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Centropages furcatus | 443 | 185 | 243 | 183 | 315 | 23 | 47 | 28 | 105 | 2 | 1 | 140 |
| Centropages hamatus | 131 | 495 | 365 | 431 | 146 | 214 | 180 | 138 | 69 | 3 | 6 | 198 |
| Clausocalanus furcatus | 48 | 2 | .... | .... | .... | .... | .... | .... | .... | .... | 1 | 8 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Clytemnestra rostrata | 5 | 4 | .... | 2 | .... | .... | .... | .... | .... | .... | .... | 1 |
| Corycaeus americanus | 178 | 65 | 49 | 13 | 5 | .... | .... | .... | 2 | .... | .... | 28 |
| Corycaeus amazonicus | 62 | 20 | 5 | 5 | .... | .... | .... | .... | .... | .... | .... | 8 |
| Corycaeus giesbrechti | 25 | .... | .... | 4 | .... | .... | .... | .... | 3 | .... | .... | 3 |
| Corycaeus latus | .... | 5 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Corycaeus speciosus | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Corycaeus spp. (immatures) | 586 | 235 | 80 | 114 | 32 | 24 | 6 | .... | .... | .... | .... | 98 |
| Corycella carinata | .... | 3 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eucalanus pileatus | 107 | 59 | 37 | 9 | 2 | .... | .... | .... | 19 | .... | .... | 21 |
| Euterpina acutifrons | 658 | 593 | 567 | 509 | 215 | 41 | 63 | 60 | 161 | 6 | 26 | 263 |
| Harpacticoids (benthic) | 55 | 46 | 56 | 59 | 32 | 53 | 17 | 63 | 31 | 7 | 17 | 40 |
| Hemicyclops type immatures | 7 | 16 | 24 | 19 | 36 | 136 | 9 | 146 | 29 | .... | 33 | 45 |
| Kelleria sp. | 97 | 2 | 8 | 2 | 1 | .... | .... | 36 | 4 | .... | .... | 14 |
| Labidocera aestiva | 59 | 173 | 98 | 110 | 52 | 92 | 98 | 36 | 53 | 2 | 2 | 70 |
| Microsetella norvegica | 8 | 11 | .... | .... | .... | .... | .... | .... | .... | .... | .... | 2 |
| Oithona brevicornis | 930 | 5557 | 6678 | 5760 | 6631 | 3609 | 2974 | 5523 | 5097 | 450 | 2715 | 4183 |
| Oithona nana | 3219 | 2857 | 1358 | 1774 | 216 | 139 | 188 | 20 | 190 | 6 | 54 | 911 |
| Oithona plumifera | 20 | 13 | .... | 2 | .... | .... | 2 | .... | .... | .... | .... | 3 |
| Oithona simplex | 400 | 836 | 547 | 349 | 149 | 37 | 34 | 1 | 19 | 2 | 6 | 216 |
| Oncaea curta | 418 | 355 | 62 | 72 | 42 | 3 | 6 | .... | 4 | 2 | 5 | 88 |
| Oncaea venusta | 15 | 22 | .... | .... | .... | .... | .... | .... | .... | .... | .... | 3 |
| Paracalanus aculeatus | 7 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 1 |
| Paracalanus crassirostris | 5619 | 8161 | 8352 | 7992 | 7597 | 6396 | 5248 | 14096 | 5319 | 479 | 1635 | 6445 |
| Paracalanus parvus | 1126 | 612 | 383 | 287 | 130 | 41 | 24 | 6 | 110 | 17 | 17 | 251 |
| Pseudodiaptomus coronatus | .... | 7 | 26 | 17 | 87 | 82 | 114 | 446 | 299 | 123 | 241 | 131 |
| Temora stylifera | 4 | 2 | .... | .... | .... | .... | .... | .... | .... | .... | .... | 1 |
| Temora turbinata | 224 | 83 | 173 | 46 | 43 | 2 | 21 | 4 | 22 | 4 | 4 | 57 |
| Tortanus setacaudatus | 3 | 3 | 23 | 5 | 25 | 19 | 37 | 6 | 41 | 1 | 62 | 21 |
| Undinula vulgaris | 4 | 5 | .... | .... | 1 | .... | .... | .... | .... | .... | .... | 1 |
| Copepod nauplii | 2498 | 4543 | 6119 | 6067 | 6626 | 5508 | 4198 | 9616 | 5367 | 2361 | 5027 | 5266 |
| CLADOCERA | | | | | | | | | | | | |
| Evadne tergestina | 321 | 296 | 213 | 294 | 476 | 528 | 925 | 208 | 456 | 48 | 255 | 366 |
| Penilia avirostris | 120 | 105 | 177 | 35 | 87 | 12 | 10 | + | 82 | 4 | 16 | 59 |
| Podon polyphemoides | 31 | 88 | 617 | 318 | 404 | 468 | 522 | 119 | 420 | 214 | 57 | 296 |
| OSTRACODA | | | | | | | | | | | | |
| Euconchoecia chierchiae | 87 | 41 | 6 | 2 | + | .... | 1 | .... | 1 | .... | 1 | 13 |
| AMPHIPODA | | | | | | | | | | | | |
| Hyperia atlantica | 6 | 2 | 1 | .... | .... | 2 | .... | .... | .... | .... | .... | 1 |
| Simorhynchotus antennarius | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| MYSIDACEA | | | | | | | | | | | | |
| Gastrosaccus dissimilis | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |

TABLE 10—Continued

Zooplankton numbers/m³ by station in the St. Andrew Bay System (1961–62 average values) Stations arranged in order of decreasing mean annual salinity + indicates observed in sample but not in aliquot

| | S3 | S2 | E4 | S1 | E3 | W2 | N2 | W1 | E2 | N1 | E1 | Avg. 1961–62 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Metamysidopsis munda | .... | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Mysidopsis almyra | .... | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| DECAPODA | | | | | | | | | | | | |
| Lucifer faxoni | 56 | 20 | 26 | 6 | 7 | 4 | 1 | .... | + | .... | + | 11 |
| CHAETOGNATHA | | | | | | | | | | | | |
| Sagitta enflata | 18 | 5 | 4 | 2 | 1 | .... | + | .... | .... | .... | .... | 3 |
| Sagitta helenae | 1 | .... | 1 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Sagitta hispida | 8 | 4 | + | 3 | 2 | 2 | 2 | 9 | 5 | .... | + | 3 |
| Sagitta tenuis | 56 | 42 | 39 | 27 | 12 | 13 | 12 | 3 | 5 | .... | 1 | 19 |
| Sagitta < 3 mm | 458 | 364 | 222 | 196 | 88 | 123 | 52 | 112 | 52 | 2 | 16 | 155 |
| APPENDICULARIA | | | | | | | | | | | | |
| Appendicularia sicula | + | 28 | 32 | 20 | + | 2 | + | .... | + | .... | .... | 7 |
| Fritillaria borealis | 25 | + | .... | 11 | .... | .... | .... | .... | .... | .... | .... | 3 |
| Fritillaria formica | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Fritillaria haplostoma | + | + | + | + | + | .... | + | .... | .... | .... | .... | .... |
| Oikopleura dioica | 774 | 1107 | 2580 | 2729 | 2795 | 3420 | 3649 | 3782 | 3801 | 1933 | 3631 | 2746 |
| Oikopleura cornutogastra | 1 | .... | .... | .... | .... | .... | .... | .... | 9 | .... | .... | 1 |
| Oikopleura fusiformis | 452 | 176 | 168 | 109 | 126 | 6 | 30 | .... | 24 | .... | 42 | 101 |
| Oikopleura longicauda | 886 | 624 | 372 | 456 | 786 | 108 | 49 | .... | 164 | .... | .... | 313 |
| Oikopleura rufescens | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Kowalevskaia tenuis | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| THALIACEA | | | | | | | | | | | | |
| Cyclosalpa floridana | + | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Dolioletta gegenbauri | 23 | 15 | 9 | 1 | 3 | .... | .... | .... | .... | .... | .... | 5 |
| LARVAE | | | | | | | | | | | | |
| Polychaete | 797 | 578 | 594 | 798 | 744 | 1150 | 593 | 1995 | 979 | 118 | 258 | 782 |
| Gastropod | 683 | 606 | 2912 | 643 | 2218 | 1721 | 1228 | 1597 | 525 | 120 | 79 | 1124 |
| Pelecypod | 2420 | 1408 | 2369 | 1277 | 894 | 2067 | 582 | 3905 | 257 | 113 | 71 | 1397 |
| Cirriped | 117 | 166 | 107 | 288 | 89 | 86 | 230 | 56 | 331 | 576 | 411 | 223 |
| Decapod | 318 | 254 | 137 | 128 | 163 | 144 | 60 | 74 | 60 | 5 | 17 | 124 |
| Echinoderm | 450 | 372 | 718 | 672 | 886 | 1163 | 278 | 4326 | 392 | 26 | .... | 834 |
| Other invertebrate | 58 | 86 | 72 | 78 | 66 | 59 | 64 | 211 | 28 | 12 | 9 | 67 |
| Cephalochordate | 21 | 5 | 1 | 3 | 1 | 1 | 1 | .... | 4 | .... | .... | 2 |
| Fish eggs | 2 | 8 | 5 | 15 | 58 | 18 | 5 | 17 | 35 | 3 | 32 | 19 |
| Fish larvae | 5 | 3 | 7 | 5 | 7 | 7 | 11 | 26 | 12 | 3 | 13 | 8 |

TABLE 11

Zooplankton dry weight (mg/m³) distribution by station in the St. Andrew Bay System (1961–62 average values)
Stations arranged in order of decreasing mean annual salinity

| | S3 | S2 | E4 | S1 | E3 | W2 | N2 | W1 | E2 | N1 | E1 | Avg. 1961–62 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DINOFLAGELLATA | | | | | | | | | | | | |
| Noctiluca scintillans | 1.74 | 2.03 | .33 | 1.16 | .93 | 2.35 | .61 | .97 | .03 | 1.19 | .01 | 1.03 |
| TINTINNOINEA | | | | | | | | | | | | |
| Tintinnopsis radix | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Stylicauda platensis | .. . | .01 | .02 | .07 | .02 | .02 | .04 | .02 | .02 | .01 | .... | .02 |
| Tintinnopsis kofoidi | .... | .... | .... | .... | .... | .. . | .... | .... | .... | .... | .... | .... |
| Tintinnopsis beutschlii | .... | .... | .... | .... | .... | .... | .... | .. . | .... | .... | .... | .... |
| Tintinnopsis brandti | .... | .... | .... | .... | .... | .... | .01 | .01 | .... | .... | .... | .... |
| Tintinnidium mucicola | .... | .... | .... | .... | .... | .02 | .05 | .01 | .... | .06 | .... | .01 |
| Eutintinnus medius | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eutintinnus pinguis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Codonellopsis obesa | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Helicostomella subulata | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Amphorides amphora | .... | .... | .... | .... | .. . | .... | .... | .... | .... | .... | .... | .... |
| Favella panamensis | .... | .... | .02 | .... | .03 | .... | .... | . .. | .14 | .... | .... | .02 |
| Favella taraikaensis | .... | .... | .... | .... | .... | .02 | .04 | .01 | .... | .01 | .... | .... |
| HYDROMEDUSAE | | | | | | | | | | | | |
| Aglaura hemistoma | .01 | .... | .... | .... | .... | .... | | | | | | |
| Bougainvillia carolinensis | .03 | .02 | .03 | .01 | .01 | .02 | .... | .... | .... | .... | .... | .01 |
| Cunina octonaria | .10 | .01 | .02 | .... | .... | .... | .... | .... | .... | .... | .... | .01 |
| Dipurena ophiogaster | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Dipurena strangulata | .... | .01 | .01 | .... | .... | .... | . . | .02 | .... | .... | .... | .... |
| Ectopleura dumortieri | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eirene pyramidalis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eucheilota duodecimalis | .07 | .03 | .08 | .02 | .06 | .05 | .03 | .03 | .02 | .... | .02 | .04 |
| Eucheilota ventricularis | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Euphysa aurata | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | ... | .... |
| Euphysora gracilis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eutima variabilis | .... | .... | .... | .... | .... | .... | .01 | .... | .06 | .... | .... | .01 |
| Halitiara formosa | . . | .... | .... | .... | .... | . . | .... | .... | .... | .... | .... | . |
| Liriope tetraphylla | .23 | .14 | .34 | .01 | .02 | .04 | .... | .28 | .01 | .... | .... | .10 |
| Nemopsis bachei | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Obelia spp. | .... | . . | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Persa incolorata | .03 | .02 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .01 |

TABLE 11 (Continued)

Zooplankton dry weight (mg/m³) distribution by station in the St. Andrew Bay System (1961–62 average values)
Stations arranged in order of decreasing mean annual salinity

| | S3 | S2 | E4 | S1 | E3 | W2 | N2 | W1 | E2 | N1 | E1 | Avg. 1961–62 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phialidium folleatum | .09 | .04 | .33 | .08 | .10 | .03 | .12 | .03 | .02 | .... | .02 | .08 |
| Phialucium carolinae | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Podocoryne minima | .... | .01 | .04 | .01 | .08 | .... | .... | .03 | .13 | .01 | .09 | .04 |
| Podocoryne minuta | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Proboscidactyla ornata | .04 | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Rhopalonema velatum | .03 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Sarsia sp. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Solmaris sp. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| SIPHONOPHORA | | | | | | | | | | | | |
| Agalma sp. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Bassia bassensis | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Diphyes dispar | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Enneagonum hyalinum | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Muggiaea kochi | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| ROTIFERA | | | | | | | | | | | | |
| Synchaeta sp. | .... | .... | .05 | .03 | .87 | .51 | .40 | .38 | .76 | .99 | 1.05 | .46 |
| Trichocerca marina | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Rotifer C | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| MOLLUSCA | | | | | | | | | | | | |
| Creseis acicula | .65 | .07 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .06 |
| Desmopterus papilio | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Pteropod A | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Protatlanta souleyeti | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| POLYCHAETA | | | | | | | | | | | | |
| Tomopteris mariana | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| COPEPODA | | | | | | | | | | | | |
| Acartia tonsa | .65 | 2.32 | 7.38 | 4.98 | 7.75 | 9.93 | 9.66 | 14.42 | 16.40 | 6.10 | 13.01 | 8.42 |
| Anomalocera ornata | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Calanopia americana | .05 | .02 | .... | .01 | .... | .... | .... | .... | .01 | .... | .... | .01 |
| Candacia sp. (immatures) | .... | .... | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Centrophages furcatus | 2.19 | .58 | .39 | .36 | .65 | .08 | .07 | .04 | .15 | .... | .01 | .41 |
| Centrophages hamatus | .23 | 1.10 | .83 | .96 | .34 | 41 | .29 | .52 | .12 | .... | .03 | .44 |
| Clausocalanus furcatus | .32 | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .04 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Clytemnestra rostrata | .01 | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Corycaeus americanus | .63 | .22 | .17 | .05 | .02 | .... | .... | .... | .... | .... | .... | .10 |
| Corycaeus amazonicus | .24 | .06 | .02 | .02 | .... | .... | .... | .... | .... | .... | .... | .03 |
| Corycaeus giesbrechti | .11 | .... | .... | .02 | ... | ... | .... | .... | .01 | .... | .... | .10 |
| Corycaeus latus | .... | .04 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Corycaeus speciosus | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Corycaeus spp. (immatures) | .73 | .20 | .08 | .10 | .02 | .02 | .01 | .... | .... | .... | .... | .11 |
| Corycella carinata | .. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Eucalanus pileatus | 1.09 | 1.28 | .86 | .36 | .01 | .... | .... | .... | .43 | .... | .... | .36 |
| Euterpina acutifrons | 1.00 | .70 | .77 | .46 | .24 | .04 | .05 | .07 | .13 | .01 | .02 | .32 |
| Harpacticoids (benthic) | .08 | .03 | .06 | .04 | .04 | .04 | .01 | .04 | .03 | .01 | .01 | .04 |
| Hemicyclops type immatures | .01 | .02 | .03 | .02 | .03 | .12 | .01 | .12 | .04 | .... | .03 | .04 |
| Kelleria sp. | .23 | .... | .03 | .... | .... | .... | .... | .05 | .... | .... | ... | .03 |
| Labidocera aestiva | .49 | .48 | .34 | .28 | .08 | .24 | .25 | .21 | .08 | .... | .... | .22 |
| Microsetella norvegica | .01 | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Oithona brevicornis | .70 | 4.17 | 5.32 | 4.40 | 5.12 | 2.81 | 2.33 | 4.43 | 4.24 | .34 | 2.33 | 3.28 |
| Oithona nana | 2.81 | 2.43 | 1.21 | 1.60 | .17 | .13 | .15 | .01 | .14 | .01 | .04 | .79 |
| Oithona plumifera | .02 | .02 | .... | .... | .. | .... | .01 | .... | .... | .... | .... | ... |
| Oithona simplex | .30 | .63 | .43 | .28 | .11 | .03 | .03 | .... | .02 | .... | .01 | .17 |
| Oncaea curta | .39 | .33 | .07 | .06 | .03 | .... | .01 | .... | .... | .... | .... | .08 |
| Oncaea venusta | .05 | .05 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .01 |
| Paracalanus aculeatus | .07 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .01 |
| Paracalanus crassirostris | 5.33 | 7.28 | 7.18 | 6.51 | 6.87 | 5.28 | 4.89 | 8.68 | 4.90 | .51 | 1.66 | 5.37 |
| Paracalanus parvus | 2.95 | 1.49 | .78 | .70 | .13 | .10 | .02 | .01 | .17 | .02 | .04 | .59 |
| Pseudodiaptomus coronatus | ... | .01 | .04 | .03 | .11 | .12 | .14 | .59 | .37 | .11 | .25 | .16 |
| Temora stylifera | .16 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .02 |
| Temora turbinata | .69 | .39 | .34 | .17 | .13 | .... | .03 | .01 | .05 | .... | .01 | .17 |
| Tortanus setacaudatus | .02 | .01 | .03 | .03 | .04 | .04 | .12 | .02 | .06 | .... | .15 | .05 |
| Undinula vulgaris | .86 | .60 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .13 |
| Copepod nauplii | 1.38 | 2.39 | 2.83 | 2.98 | 2.90 | 2.49 | 2.15 | 3.83 | 2.53 | 1.29 | 2.45 | 2.47 |
| CLADOCERA | | | | | | | | | | | | |
| Evadne tergestina | .39 | .36 | .26 | .36 | .57 | .63 | 1.11 | .25 | .55 | .06 | .31 | .44 |
| Penilia avirostris | .20 | .18 | .30 | .06 | .15 | .02 | .02 | .. | .14 | .01 | .03 | .10 |
| Podon polyphemoides | .03 | .08 | .57 | .29 | .37 | .43 | .48 | .11 | .39 | .20 | .05 | .27 |
| OSTRACODA | | | | | | | | | | | | |
| Euconchoecia chierchiae | .47 | .17 | .01 | .... | .... | .... | .... | .... | .... | .... | .... | .06 |
| AMPHIPODA | | | | | | | | | | | | |
| Hyperia atlantica | .15 | .04 | .03 | .... | .... | .05 | .... | .... | .... | .... | .... | .02 |
| Simorhynchotus antennarias | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| MYSIDACEA | | | | | | | | | | | | |
| Gastrosaccus dissimilis | .. | .. | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |

TABLE 11 (Continued)

Zooplankton dry weight (mg/m³) distribution by station in the St. Andrew Bay System (1961–62 average values)
Stations arranged in order of decreasing mean annual salinity

| | S3 | S2 | E4 | S1 | E3 | W2 | N2 | W1 | E2 | N1 | E1 | Avg. 1961–62 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Metamysidopsis munda | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Mysidopsis almyra | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| DECAPODA | | | | | | | | | | | | |
| Lucifer faxoni | .79 | .30 | .26 | .07 | .06 | .04 | .01 | .... | .... | .... | .... | .14 |
| CHAETOGNATHA | | | | | | | | | | | | |
| Sagitta enflata | .48 | .09 | .06 | .02 | .07 | .... | .... | .... | .... | .... | .... | .07 |
| Sagitta helenae | .04 | .... | .01 | . . | . | . | .... | .... | .... | .... | .... | .01 |
| Sagitta hispida | .30 | .10 | .01 | .06 | .07 | .11 | .03 | .26 | .07 | .... | .... | .10 |
| Sagitta tenuis | .80 | .66 | .60 | .29 | .16 | .21 | .08 | .04 | .09 | . .. | .01 | .27 |
| Sagitta <3mm | 1.05 | .51 | .37 | .30 | .12 | .20 | .11 | .16 | .07 | .... | .02 | .27 |
| APPENDICULARIA | | | | | | | | | | | | |
| Appendicularia sicula | .... | .02 | .03 | .01 | .... | .... | .... | .... | .... | .... | .... | .01 |
| Fritillaria borealis | .06 | . .. | .... | .01 | .... | . . | .... | .... | .... | .... | .... | .01 |
| Fritillaria formica | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Fritillaria haplostoma | .... | .... | .... | .... | . | .... | .... | .... | .... | .... | . . | .... |
| Oikopleura dioica | 1.49 | 1.72 | 3.83 | 4.20 | 3.55 | 4.39 | 4.57 | 3.70 | 4.13 | 2.25 | 4.72 | 3.51 |
| Oikopleura cornutogastra | .01 | .... | . . | . . | . . | . | . . | .... | .02 | .... | .... | .... |
| Oikopleura fusiformis | .88 | .28 | .20 | .14 | .21 | .01 | .05 | .... | .03 | .... | .13 | .17 |
| Oikopleura longicauda | 1.38 | .87 | .53 | .50 | 1.13 | .10 | .08 | .... | .22 | .... | .... | .44 |
| Oikopleura rufescens | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Kowalevskaia tenuis | .... | .... | . .. | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| THALIACEA | | | | | | | | | | | | |
| Cyclosalpa floridana | .... | .... | .... | .... | . . | .... | .... | .... | .... | .... | .... | . . |
| Dolioletta gegenbauri | .35 | .11 | .10 | .... | .02 | .... | .... | .... | .... | .... | ... | .05 |
| LARVAE | | | | | | | | | | | | |
| Polychaete | 2.95 | 2.14 | 2.20 | 2.95 | 2.75 | 4.25 | 2.19 | 7.38 | 3.62 | .44 | .96 | 2.89 |
| Gastropod | 1.82 | 1.62 | 7.75 | 1.71 | 5.90 | 4.58 | 3.27 | 4.25 | 1.40 | .32 | .21 | 2.98 |
| Pelecypod | 6.44 | 3.68 | 6.30 | 3.40 | 2.38 | 5.50 | 1.55 | 10.39 | .68 | .28 | .19 | 3.71 |
| Cirriped | .33 | .42 | .20 | .39 | .21 | .18 | .23 | .09 | .41 | .58 | .41 | .31 |
| Decapod | 1.72 | 1.38 | .74 | .70 | .89 | .78 | .31 | .40 | .32 | .03 | .09 | .67 |
| Echinoderm | .14 | .11 | .19 | .18 | .23 | .30 | .08 | 1.13 | .10 | .01 | . | .23 |
| Other invertebrate | .05 | .06 | .... | .01 | . | . | .... | .06 | .01 | .... | .01 | .01 |
| Cephalochordate | .09 | .02 | . .. | .01 | .01 | .01 | .... | .... | .02 | . | . | .01 |
| Fish eggs | .02 | .07 | .04 | .13 | .51 | .16 | .05 | .15 | .30 | .03 | .28 | .17 |
| Fish larvae | .03 | .02 | .05 | .04 | .04 | .05 | .08 | .17 | .08 | .02 | .08 | .05 |

tion to total zooplankton number (0.16%) and biomass (0.71%). The four most important species which together composed 82% of the hydromedusae biomass were *Liriope tetraphylla* (Chamisso and Eysenhardt) (32.2%), *Phialidium folleatum* (McCrady) (25.3%), *Eucheilota duodecimalis* A. Agassiz (12.2%), and *Podocoryne minima* (Trinci) (11.8%).

Seasonally, total hydromedusae numbers were largest in February 1960 and in November 1961. The biomass peak (Fig. 4 B) occurred in September of 1961. In 1961–62, 18 species were either seen more frequently or gave higher counts in aliquots of samples taken during the warmer months (25–29 C). These species were *Aglaura hemistoma* Péron and Lesueur, *Bougainvillia carolinensis* (McCrady), *Cunina octonaria* McCrady, *Dipurena ophiogaster* Haeckel, *Dipurena strangulata* McCrady, *Eirene pyramidalis* (L. Agassiz), *Eucheilota duodecimalis*, *Eucheilota ventricularis* McCrady, *Euphysora gracilis* (Brooks), *Eutima variabilis* McCrady, *Halitiara formosa* Fewkes, *Liriope tetraphylla*, *Obelia* sp. (spp.?), *Phialidium folleatum*, *Phialucium carolinea* (Mayer), *Podocoryne minuta* (Mayer), *Rhopalonema velatum* Gegenbaur, and *Solmaris* sp. The remaining species (*Ectopleura dumortieri* (van Beneden), *Euphysa aurata* Forbes, *Persa incolorata* McCrady, *Podocoryne minima*, *Proboscidactyla ornata* (McCrady), *Sarsia* sp.) appeared more frequently in the cooler half of 1961–62 (11–22 C).

Eighteen of the 25 species seen in 1961–62 appeared previously in 1959–60 samples. Only a single species, *Nemopsis bachei* L. Agassiz, was taken in 1959–60 but not in 1961–62. Though data for 1959–60 are less complete, it is clear that the seasonal picture for this year does not correspond well with that of 1961–62. The greatest variety of hydromedusae in 1959–60 was recorded for February whereas in 1961–62 the greatest diversity occurred in the warmer months. Species which were more prevalent in the cooler months of both years were *E. dumortieri*, *P. incolorata*, and *P. minima*.

Geographically, greatest variety was found at station S3, the sampling point nearest the Gulf. Twelve species (*B. carolinensis*, *C. octonaria*, *E. dumortieri*, *E. pyramidalis*, *E. ventricularis*, *E. gracilis*, *L. tetraphylla*, *P. incolorata*, *P. minuta*, *P. ornata*, *R. velatum*, *Solmaris* sp.) were more prevalent at this station than at any other. These species along with *E. aurata*, *H. formosa*, and *P. folleatum* were more abundant at the four stations nearest the Gulf (29–33 ppt) than at all other stations combined. The remaining species (*E. duodecimalis*, *E. variabilis*, *D. ophiogaster*, *D. strangulata*, *N. bachei*, *Obelia* sp. (spp.?), *P. carolinae*, *P. minima*, *Sarsia* sp.) were taken more often at stations farther into the estuaries (19–27 ppt). One species, *Aequorea macrodactyla* (Brandt), while not collected in the bay system, was seen in a sample taken near station S3 on the Gulf side of West Pass.

According to Kramp's (1961) synopsis and to Sears (1954) all but three species (*E. dumortieri*, *E. aurata*, *P. minima*) have previously been reported from the Tortugas and coastal waters of the southeastern United States.

**Siphonophores:** Siphonophores were not conspicuously abundant. This group comprised only 0.01% of total zooplankton number and 0.04% of the dry weight. Nectophores of *Muggiaea kochi* (Will) constituted 23.4% of the total number of bracts, eudoxids, and nectophores found in aliquots. The remainder was largely unidentified because of their small size and poor state of preservation. Three other siphonophores, *Bassia bassensis* Quoy and Gaimard, *Diphyes dispar* Chamisso and Eysenhardt, and *Enneagonum hyalinum* Quoy and Gaimard, were seen in several collections but did not

occur in aliquots. Dr. Mary Sears (personal communication) also found two bracts of *Diphyes bojani* (Eschscholtz) among specimens picked from aliquots. Agalmid persons were occasionally enountered but were not identified.

No seasonal trend for total numbers of siphonophores was evident though it is worth noting that *Muggiaea kochi* was more abundant in warmer months. Siphonophores generally did not penetrate far into the bay and were rarely seen at stations beyond S1 and E4. An exception occurred in November 1959 when bracts were carried as far into the bay as E2.

**Rotifers:** The three kinds of rotifers caught with #10 nets were *Synchaeta* sp., *Trichocerca marina* (Daday), and an unidentified rotifer. *Synchaeta* sp. was the most abundant species and was large enough for dry weight estimates. *Synchaeta* appeared in the winter (Fig. 4 A), making its first appearance in 1961–62 in November. Maximum abundance occurred in January (19,300/$m^3$). The number dropped sharply in February (12/$m^3$) and *Synchaeta* disappeared completely by June. Counts of this rotifer in quarterly survey samples suggest that a similar cycle occurred in 1959–60. *Trichocerca marina*, appeared sporadically throughout 1961–62 and was found in November and February samples of 1959–60. The unidentified rotifer occurred in November, January, and May samples of 1961–62 and in November and February samples of 1959–60.

*Synchaeta* was most abundant at stations near the heads of East and North Bays and least abundant at the four stations nearest the Gulf. This rotifer, then, may be a true estuarine species. Although the other two species were taken less frequently, it appears that they, too, were least abundant at high salinity stations.

Rotifers made a significant contribution to zooplankton numbers and in 1961–62, with an average of almost 5% of the total catch. The numerical importance of rotifers undoubtedly has been underestimated since both *Trichocerca* and the unidentified rotifer easily can pass through the meshes of #10 nets. The biomass contribution of *Synchaeta* to total zooplankton biomass alone was 1.07%. Weights of the other two species were not determined.

**Molluscs and polychaetes:** Molluscs were represented by the pteropods *Creseis acicula* Rang, *Desmopterus papilio* Chun, and an unidentified gymnosomatous form and by the heteropod *Protatlanta souleyeti* (E.A. Smith). Of the three pteropods only *Creseis acicula* appeared commonly in aliquots. *Creseis* was taken in August and June of 1959–60 and appeared in every month of 1961–62 except February. It was generally more prevalent in the warmer months (April–October 1961) and showed maxima in June 1960 and April 1962. *Creseis* was most abundant at S3, the station nearest the Gulf, and its numbers declined sharply with decreasing mean salinity. In one instance it was collected as far into East Bay as E2 (September 1961). *Desmopterus papilio* was taken at S3 in August 1961 and the gymnosomatous pteropod was collected at S2 in August 1961, and at S3 and E4 in September 1961. *Protatlanta* was seen in February and June samples of 1960 and was encountered again in August and June samples of 1961–62. This species was taken only at S3, S2, and E4. Because of the eroded condition of the specimens the identification of this atlantid must remain tentative (Mr. Norman Tebble, personal communication).

Only one species of holoplanktonic polychaete, *Tomopteris mariana* Greeff, was found in St. Andrew Bay. It was an uncommon plankter and never exceeded five individuals/$m^3$. This polychaete was not recorded at all for 1959–60, and was seen only a few times

in samples collected in September, October, and May-June of 1961–62. *T. mariana* was taken at sampling points no farther into the bay complex than E3 and S1.

The contribution of holoplanktonic molluscs and polychaetes together was small and constituted only 0.1% of the total zooplankton count. Specimens of *Tomopteris* were too scarce to weigh and all that were sorted were used for identification purposes. *Creseis* on the other hand, was abundant enough to permit dry weight analysis and this species averaged 0.13% of the total zooplankton dry weight (inorganic shell weight included).

**Copepods:** Copepods, as in many other surveys, constituted the most important zooplankton group, averaging 59.0% of the total number and 55.8% of the total dry weight in 1961–62. Peak numbers of copepods and nauplii occurred in November and June of 1959–60 and in June and August of 1961–62. Minima were recorded for August of 1959 and February of 1962. Copepod biomass maxima in 1961–62 (Fig. 4 C) appeared in September and August while the minimum, which corresponded with the numerical low, occurred in February. Populations were largest at W1 near the head of West Bay and smallest at N1 in North Bay.

Thirty species of copepods were identified from aliquots. These species check well with those previously listed by Grice (1957) for St. Andrew Bay. Thirteen of the thirty individually averaged more than 1% of both the copepod number and weight at one station or another. Seven of these thirteen, *Centropages furcatus* (Dana), *Corycaeus americanus* M. S. Wilson, *Euterpina acutifrons* (Dana), *Oithona nana* Giesbrecht, *Oncaea curta* Sars, *Paracalanus parvus* (Claus), and *Temora turbinata* (Dana), were most numerous at S3, the sampling point nearest the Gulf. Two, *Oithona simplex* Farran and *Centropages hamatus* (Lilljeborg), were most abundant at S2 which is three miles farther into the bay than S3. Three more of the thirteen, *Paracalanus crassirostris* Dahl, *Pseudodiaptomus coronatus* Williams, and *Acartia tonsa* Dana were most abundant in the upper reaches of West Bay (W1), though populations of *Acartia* were almost as large near the head of East Bay (E1, E2). Finally, *Oithona brevicornis* Giesbrecht was taken in greatest quantities in East Bay (E3, E4). The latter species seems to thrive best in estuarine conditions as do *Acartia tonsa*, *Paracalanus crassirostris*, *Pseudodiaptomas coronatus*, and *Tortanus setacaudatus* Williams (a species of lesser importance).

Data on seasonal distribution of copepods in 1961–62 reveal that annual maxima for ten of the 13 most abundant species occurred during the warmest months of the year, *i.e.*, May–September (25–29 C). Four species, *E. acutifrons*, *P. parvus*, *O. nana*, and *A. tonsa* were numerically most abundant in late spring. Four other species, *P. crassirostris*, *O. brevicornis*, *C. americanus*, and *C. furcatus*, were most abundant in the summer and two species, *T. turbinata* and *P. coronatus* were taken in greatest numbers in early fall. Maxima during the warmer months were also observed in populations of three less prominent species, *Eucalanus pileatus* Giesbrecht, *Tortanus setacaudatus*, and *Labidocera aestiva* Wheeler. Only *O. simplex* and *O. curta* were most abundant in late fall and *C. hamatus* alone achieved a maximum in mid-winter. Of the copepods which were most abundant in the warmer months, *T. turbinata*, *C. americanus*, *P. parvus*, *O. nana*, *L. aestiva*, and *A. tonsa* also had peaks in the cooler months of the year, *i.e.*, November–March (11–22 C). *Acartia*, in fact, was nearly as abundant in January as in May. Peaks in warmer months, at least, for *C. furcatus* and *T. setacaudatus* and in the cooler months for *C. hamatus* would be expected since a rather distinct seasonal pattern of abundance in northern Gulf waters has already been reported (Grice, 1957) for these species. The

principal maxima for the total copepod population appeared in August and June, though a lesser peak was noted in January. The minimum for the year was recorded for February. The decline of the copepod population in this month was apparently the result of a sharp drop in the numbers of *A. tonsa*. Of the thirteen most abundant species, eleven were found at their annual minimum in February.

Quarterly survey data reveal a different copepod seasonal picture for 1959–60. Seven of the 13 species mentioned above were less abundant in the summer collections than in the late fall and winter surveys. Also, smallest catches of copepods were obtained in August instead of in February.

Considering overall averages for the entire bay complex, *Acartia tonsa* was the most abundant copepod averaging 39.4% of the copepod biomass (exclusive of nauplii). Dominance of *A. tonsa* in St. Andrew Bay estuaries is not surprising since the importance of this species in brackish waters from southern New England to southern Florida and to Texas has been well documented (Sutcliffe, 1948; Deevey, 1948, 1956, 1960; Grice, 1953, 1957; Breuer, 1962; Cronin *et al.*, 1962; Cuzon du Rest, 1963). The two next most important species were *Paracalanus crassirostris* (25.1%) and *Oithona brevicornis* (15.3%). These species together with *Acartia* composed the bulk (80%) of the copepod stock. Of the remaining species only *Oithona nana* (3.7%), *Paracalanus parvus* (2.7%), *Centropages hamatus* (2.1%), *Centropages furcatus* (1.9%), *Eucalanus pileatus* (1.9%), and *Euterpina acutifrons* (1.5%) exceeded 1% of the dry weight of the copepod standing crop.

**Other crustaceans:** Cladocerans were often abundant in the plankton of the St. Andrew Bay System. These crustaceans in 1961–62 averaged 1.8% of the total number and 1.9% of the total zooplankton biomass. Population maxima occurred in June of the 1959–60 quarterly investigation and in August and January of the monthly 1961–62 survey. Minima were recorded for November of 1959 and for December and February of 1961–62. Biomass peaks for 1961–62 (Fig. 4 D) corresponded with numerical peaks for this sampling year and occurred in August and January. Biomass minima in 1961–62 were recorded for December and February.

Three species of cladocerans, *Evadne tergestina* Claus, *Penilia avirostris* Dana, and *Podon polyphemoides* (Leuckart), were taken in the plankton hauls. *Evadne* and *Penilia* were collected in the warmer months and were scarce or absent from December through April. A similar distribution for *Evadne* and *Penilia* was observed at Alligator Harbor, Florida by Grice (1953). Peak numbers of *Evadne* appeared in June 1960 and in August 1961. During the warmer months *Evadne* became well established throughout the bay system and was especially abundant at N2 close to the mouth of North Bay. *Evadne* was least abundant in the bay system at N1 near the head of North Bay. *Penilia* populations were largest in June 1960 and in September 1961. This cladoceran was most abundant at stations nearest the Gulf and was better represented in East Bay than in North or West Bays. *Podon polyphemoides*, a cool water species according to Baker (1938), was taken in numbers from December through May. *Podon* was found in greatest quantities in the June survey of 1960 and in January and March of 1962. As was true for many species of copepods, there was a significant drop in counts of this cladoceran in February 1962. Largest populations of *Podon* were at stations of mean salinities between 23–30 ppt with heaviest concentrations occurring at E4 (29.7 ppt). *Podon* was taken in fewest numbers

at E1 (19.4 ppt) and S3 (32.7 ppt), stations with mean salinities on either side of the above salinity range.

Only one holoplanktonic ostracod, *Euconchoecia chierchiae* Müller, was taken in St. Andrew Bay. It is a coastal form which has been reported from the coasts of Brazil and North Carolina and from Delaware Bay and Block Island Sound (Deevey, 1952, 1960). This species appeared in November and February hauls of 1959–60 and was collected July through February in 1961–62. Maximum averages for *Euconchoecia* were recorded for February 1960 and August 1961. It was encountered most often at S2 and S3, stations closest to the Gulf. *Euconchoecia* was scarce at all other stations in the bay and was not taken at all at the head of North Bay (N1) and in West Bay. Benthic ostracods occasionally appeared in sample aliquots but their identifications were not pursued.

Three species of mysids were encountered in tows made from 1959–62. *Metamysidopsis munda* (Zimmer) appeared in a January (1962) sample collected in East Bay (E4), *Gastrosaccus dissimilis* Coifmann was taken in St. Andrew Bay (S1) in December 1961, and *Mysidopsis almyra* Bowman was collected at S2 in December 1961 and at S3 in June 1962. Three other species were identified from tows made near S3 prior to 1959. These species, *Promysis atlantica* Tattersall, *Taphromysis bowmani* Bacescu, and *Anchialina typica* (Krøyer), were represented, as were those taken in 1959–62, by only a few specimens per tow. *Taphromysis bowmani, M. munda, G. dissimilis* and *M. almyra* have been found previously in northern Gulf of Mexico waters (Tattersall, 1951; Bacescu, 1961; Bowman, 1964).

Since all of the tows in the 1959–62 investigations were made during daylight hours it is possible that the mysid contribution to the plankton has been underestimated. Hopkins (1958) and Herman (1963) have noted that mysids are far more abundant in the water column during periods of darkness. Herman (1963) has shown that *Neomysis americana* (S. I. Smith), an abundant mysid in coastal waters of the northern Atlantic states, is either on or just above the bottom during the day. Mysids in the St. Andrew Bay System with a behavior pattern similar to that of *Neomysis* could well have avoided capture in this investigation. This is so because the Clarke-Bumpus device was towed no closer than a foot or so above the bottom as a precaution against filling the sampler with sediment.

Amphipods constituted only a small portion of the zooplankton number and biomass. Of the two planktonic species encountered, *Hyperia atlantica* Vosseler and *Simorhynchotus antennarius* Claus, only the former appeared in sample aliquots. *Hyperia atlantica* was taken in small numbers in every season particularly at stations near the Gulf. *Simorhynchotus* was observed in a sample taken at S3 in June 1961. Gammarid amphipods were seen on occasion, though they were even less abundant than planktonic forms.

Isopods were collected throughout the year and were found at every station but N1. There was little variety in the catch and the species encountered were almost invariably Bopyridae or *Munna*. Branchiurans were captured in several East Bay tows made at E1 and E4 and a single cumacean specimen appeared in the aliquot of the June 1962 sample from S3.

The planktonic shrimp *Lucifer faxoni* Borradaile was present in St. Andrew Bay in every season, though in 1961–62 it was relatively scarce from December through April and was not seen at all in winter (February, 1960) samples of the quarterly survey.

*Lucifer* was taken most often at S3 near the Gulf and became increasingly scarce towards the heads of estuaries.

*Lucifer* along with the amphipod *Hyperia* and the ostracod *Euconchoecia* only represented 0.52% of the zooplankton biomass. Except for copepods and cladocerans these were the only planktonic crustaceans for which dry weight estimates were obtained. The combined number of all crustaceans other than copepods and cladocerans was only 0.08% of the total zooplankton number.

**Chaetognaths:** Chaetognaths were represented in the St. Andrew complex by four species, *Sagitta enflata* Grassi, *Sagitta helenae* Ritter-Zahony, *Sagitta hispida* Conant, and *Sagitta tenuis* Conant. All of these species have been recorded previously in coastal waters of the Gulf of Mexico (Pierce, 1951, 1962). Chaetognaths were most abundant during the warmer months while the population was smallest from December through April. Maxima (Fig. 4 E) were recorded for August and June of the monthly investigations while the minimum appeared in February. The average number of chaetognaths in the quarterly 1959–60 survey was about the same in August, November, and June while the population in February was comparatively small. This group totalled 0.45% of the zooplankton number and 1.66% of the zooplankton biomass.

Most of the chaetognath biomass was composed of immature forms under 3 mm in length. These immatures were not positively identified but in most instances they appeared to be the young of *S. tenuis*. The most important species of those chaetognaths larger than 3 mm was also *S. tenuis*, with *S. hispida*, *S. enflata*, and *S. helenae* following in order of importance. *Sagitta enflata*, *S. helenae*, and *S. tenuis* were most abundant at stations near the Gulf, though the latter species penetrated far into the estuaries. *Sagitta hispida* was taken throughout the bay complex and its distribution was not obviously related to distance from the Gulf. Largest averages for *S. hispida* were obtained for S3 and W1, two widely separated stations.

An earlier study of the chaetognath fauna of St. Andrew Bay was reported by Smith (1955), who sampled two stations located near S2 and S3. Smith encountered the same four species and averages for both Smith's two stations and S2 and S3 are in Table 12 below:

In both investigations, *S. tenuis* was the most abundant chaetognath, though this species was more abundant in 1961–62 than in 1954. *Sagitta enflata*, the next most important species, and *S. hispida* were found in approximately the same numbers in both years. *Sagitta helenae*, on the other hand, was noticeably more abundant in 1954 than in 1961–62. Smith found *S. helenae* to be more common at his offshore stations; perhaps the higher average for this species in 1954 is partially related to the fact that the

TABLE 12

Chaetognath abundance in 1954 and 1961–62

| | 1954 (Smith) #/m³ | 1961–62 (Hopkins) #/m³ |
|---|---|---|
| *S. hispida* | 5.4 | 5.2 |
| *S. helenae* | 6.3 | 0.5 |
| *S. tenuis* | 16.4 | 49.0 |
| *S. enflata* | 8.6 | 11.1 |
| Mean salinity | 34 ppt | 32 ppt |

mean salinity in the lower reaches of St. Andrew Bay was higher in 1954 (34 ppt) than in 1961–62 (32 ppt).

Considering Smith's 1954 data and those for 1959–60 and 1961–62, *Sagitta enflata* maxima appeared in one year or another in fall, winter, and summer. *Sagitta tenuis* maxima occurred only in summer and fall. *Sagitta hispida* peaks occurred in every season and maxima for *S. helenae* were recorded for every season but fall. In summary, *S. tenuis* was most abundant in the warmer months while seasonal patterns of the other three species were less well defined.

**Appendicularians:** Considering holoplankters alone, appendicularians were outranked in abundance only by copepods. This group in 1961–62 constituted 7.9% of the number and 9.7% of the biomass of the zooplankton. Of the ten species identified *Oikopleura dioica* Fol was by far the most common, averaging 86.5% of the appendicularian dry weight. The bulk of the remaining biomass was composed of *Oikopleura longicauda* Vogt (9.9%) and *Oikopleura fusiformis* Fol (3.2%), though *Appendicularia sicula* Fol was abundant on occasion (July 1960). Species of lesser importance were *Fritillaria borealis* f. *sargassi* Lohmann, *Fritillaria formica* Fol, *Fritillaria haplostoma* Fol, *Kowalevskaia tenuis* Fol, *Oikopleura rufescens* Fol, and *Oikopleura cornutogastra* Aida. The latter species, according to Tokioka (1940), may be a form of *O. fusiformis* and forms intermediate between these two species were encountered among St. Andrew Bay specimens (Dr. Takasi Tokioka, personal communication).

All spcies with the exception of *O. dioica* were taken in greatest numbers at stations in the more saline regions of the bay system (S3, S2, S1, E4, E3). *Oikopleura dioica,* a temperate-tropical species often reported from estuaries (Essenberg, 1926; Percival, 1929; Thompson, 1948; Barlow, 1955; Deevey, 1960) was collected throughout the bay complex and its numbers increased towards the heads of the estuaries. A conspicuous deviation from this trend is the low average number of *O. dioica* recorded for N1 which is far below the mean for stations of similar brackishness. *Appendicularia sicula,* while usually most abundant near the Gulf, appeared in numbers far into the bay complex in June 1960, reaching a density of 6600/$m^3$ at W2 in West Bay.

Though the appendicularian species found in the St. Andrew Bay System are reportedly most abundant in tropical and subtropical seas (Thompson, 1948), half of the species were encountered so infrequently and in such small numbers that little can be said of their local seasonal distribution. *Fritillaria borealis* f. *sargassi* was taken in only three months, *F. formica, F. haplostoma,* and *O. rufescens* in only two months, and *K. tenuis* and *O. cornutogastra* in but one month. *Appendicularia sicula* appeared in every season but its distribution in time may not have been continuous. The maximum count for this species was obtained in July 1960.

In regard to the more prevalent species, *O. fusiformis* was most abundant in November of the 1959–60 quarterly survey and in August, October, and April of the 1961–62 monthly investigation. This species was scarce in the February and June surveys of 1960 and from December through February in 1961–62. *Oikopleura longicauda,* perhaps the most frequently encountered appendicularian in tropical waters (Thompson, 1948), was prevalent in the warmer months and appeared in greatest densities in August and June of 1959–60 and again in August and June of 1961–62. This appendicularian was quite abundant at S3 near the Gulf where it approximated *O. dioica* in number. Minimum counts of *O. longicauda* were recorded for November and February of 1959–60 and in

December and February of 1961–62. The dominant appendicularian, *O. dioica*, like *O. longicauda*, was most abundant during the warmer months. *O. dioica* showed peaks in August and June of 1959–60 and in August and May of 1961–62. Smallest catches of *O. dioica* were obtained in February of both 1960 and 1962. Because of the relative importance of this species, total appendicularian number and biomass essentially followed the same seasonal pattern as that of *O. dioica* (Fig. 4 F).

**Thaliaceans:** The contribution of Thaliacea to zooplankton biomass was insignificant and in 1961–62 accounted for only 0.13% of the total dry weight. One doliolid, *Dolioletta gegenbauri* (Uljanin), and a single species of salp, *Cyclosalpa floridana* Apstein, were seen in 1959–62 collections. Two other salps, *Salpa cylindrica* Cuvier and *Thalia democratica* Forskal were taken near S3 in 1958. *Dolioletta gegenbauri* occurred at the five stations with the highest salinity averages and was most abundant at S3, the station nearest the Gulf. This doliolid, reportedly a eurythermal species (Thompson, 1948), was taken in every month in 1961–62 except March and April and reached peak abundance in May. In 1959–60 it was found in only August and June. A fourth thaliacean *Cyclosalpa floridana* was seen in a single sample collected in August 1961 at station S3.

**Larvae:** On the basis of dry weight, the biomass of the larvae exceeded one-fifth the zooplankton biomass caught with #10 nets. The most important contributors were mollusc veligers, which averaged 60.7%[a] of the larvae dry weight and polychaete larvae which accounted for 26.2% of the larvae biomass. Predominance of veligers and polychaete immatures in larval plankton also has been observed in Long Island Sound by Deevey (1956). The remaining invertebrate larval biomass was composed principally of decapod immatures (6.1%) cirriped larvae (2.8%), and echinoderm larvae (2.0%). Cephalochordate larvae, small fish larvae, and fish eggs totaled 2.1% of the larvae weight. Larvae for which no dry weight data are available were either scarce or, if occasionally abundant, were quite small and therefore of little consequence in biomass considerations.

Mollusc larvae were abundant throughout the entire bay complex with gastropod veliger populations being greatest in East Bay (E3, E4) and with pelecypod veligers reaching maximum concentrations in West Bay (W1). Lowest average counts for both pelecypod and gastropod larvae were obtained near the heads of East and North Bays. Larval polychaete populations were greatest in West Bay and comparatively small catches were obtained, as with veligers, in the upper reaches of North and East Bays. Decapod larvae were in greatest numbers near the Gulf (S3) and there was a general decrease in abundance with decreasing mean salinity. Smallest averages for these larvae were obtained, again, for the heads of North and East Bays. Cirriped larvae, on the other hand, were most abundant at the three stations of lowest salinity (E2, N1, E1) and least abundant at three stations of intermediate salinity. Peak values for echinoderm larvae (chiefly brachiolarians) were recorded for West Bay station W1, where counts averaged 4300/m$^3$ in 1961–62. The high mean for W1 can be attributed to the unusually high densities (49,500/m$^3$) of brachiolarians which were found at this station in June 1962. Echinoderm larvae were scarce in North Bay and were absent from E1 at the head of

[a] This value can lead to an overestimate of the relative importance of veligers in the plankton food chain since veliger dry weight also includes inorganic shell weight.

East Bay. Cephalochordates were taken most frequently near the Gulf whereas highest values for fish eggs and larvae were found for stations well into the bay system.

Seasonal maxima for mollusc, polychaete, decapod, and echinoderm larvae occurred during the warmer months (Fig. 4 G) which corresponds with the seasonal distribution of these larvae in Long Island Sound (Deevey, 1956). Cirriped larvae maxima were in the cooler months as well and were particularly abundant in February 1960.

In the 1959–60 survey gastropod veligers were most common in August and June and in the 1961–62 survey they were most abundant in September and June. Comparatively few gastropods were taken in the November survey of 1959 and from December through April in 1961–62. The principal maxima for pelecypod larvae were recorded for June of 1959 and for August and June of 1961–62. Lowest count averages were obtained from November 1959 and February 1962 samples. Polychaete larvae were taken in greatest quantities in June of both 1960 and 1962. A cool weather peak was also recorded in January of 1962. A winter (February) minimum for polychaete larvae was noted for 1962 but there was no apparent minimum in 1959–60. Decapod larvae were most numerous in August of 1959–60 and in September and June of 1961–62. They were entirely absent from samples taken in November and February of 1959–60 and were least abundant in 1961–62 from November through April. Echinoderm larvae, brachiolarians in the main, were extremely abundant in June 1962 but did not show a corresponding peak in June of 1960. A minimum occurred in November 1959, and echinoderm larvae were not seen in samples taken in February 1962. Maximum numbers of fish eggs were recorded for August and June of 1959–60 and small peaks appeared in August and May of 1961–62. Small fish larvae were taken only in August and June of 1959–60 and were most prevalent in August and June of 1961–62. The maximum total count for all larvae occurred in June of both 1959 (3300/$m^3$) and 1962 (21,700/$m^3$) while minima were recorded in November 1959 (400/$m^3$) and in February 1962 (260/$m^3$).

## TOTAL ZOOPLANKTON STANDING CROP

Contributions of the principal groups of plankters to total zooplankton standing crop are summed in Tables 13 and 14. Groups exceeding 1% of both zooplankton number and dry weight were copepods, larvae of benthic invertebrates, appendicularians, dinoflagellates, rotifers, and cladocerans. The most important of these were copepods, larvae of benthic invertebrates, and appendicularians. Together these three categories constituted 79% of the zooplankton number and 92% of the dry weight. The dominant plankters as in many other studies were the copepods. They alone accounted for 60% and 56% of the zooplankton number and dry weight respectively.

Over 50% of zooplankton numbers and 53% of the dry weight were contributed by seven species of plankton: *Acartia tonsa*, *Paracalanus crassirostris*, *Oikoplura dioica*, *Oithona brevicornis*, *Noctiluca scintillans*, *Oithona nana*, and *Synchaeta* sp. .The most important plankter in terms of dry weight was *Acartia tonsa* which accounted for 20% of the total zooplankton standing crop while the greatest numerical contribution was that of *Paracalanus crassirostris* which composed 16% of the zooplankton catch. The contributions of these copepods are underestimated since nauplii counts were not taken to species.

TABLE 13

Distribution of the major zooplanton groups by station in the St. Andrew Bay System (average 1961–62 values). Upper numbers in each row represent individuals/$m^3$; lower numbers in parentheses represent dry weight ($mg/m^3$). Stations arranged in order of decreasing mean annual salinity.

| | S3 | S2 | E4 | S1 | E3 | W2 | N2 | W1 | E2 | N1 | E1 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Dinoflagellates | 4768 | 5486 | 877 | 3127 | 2515 | 6347 | 1638 | 2632 | 85 | 3209 | 20 |
| | (1.74) | (2.03) | (.33) | (1.16) | (.93) | (2.35) | (.61) | (.97) | (.03) | (1.19) | (.01) |
| Tintinnids | 207 | 604 | 2111 | 6036 | 1530 | 2711 | 7356 | 2568 | 3081 | 4320 | 483 |
| | (<.01) | (.01) | (.04) | (.08) | (.05) | (.06) | (.13) | (.04) | (.16) | (.08) | (.01) |
| Hydromedusae | 100 | 62 | 116 | 35 | 94 | 27 | 31 | 52 | 103 | 5 | 68 |
| | (.66) | (.28) | (.86) | (.14) | (.28) | (.14) | (.17) | (.41) | (.24) | (.01) | (.13) |
| Siphonophores | 24 | 16 | 5 | 6 | .... | .... | .... | .... | .... | .... | .... |
| | (.14) | (.04) | (.01) | (.01) | .... | .... | .... | .... | .... | .... | .... |
| Rotifers | .... | 32 | 193 | 188 | 3922 | 2433 | 1823 | 1608 | 3192 | 4281 | 4387 |
| | .... | (<.01) | (.05) | (.03) | (.87) | (.51) | (.40) | (.38) | (.76) | (.99) | (1.05) |
| Molluscs & Polychaetes | 402 | 55 | 11 | 1 | 1 | .... | .... | .... | .... | .... | .... |
| | (.65) | (.07) | (<.01) | (<.01) | (<.01) | .... | .... | .... | .... | .... | .... |
| Copepods | 17392 | 26494 | 29540 | 27429 | 27853 | 22253 | 19586 | 39594 | 25469 | 6953 | 17998 |
| | (23.77) | (26.84) | (29.20) | (24.43) | (24.80) | (21.89) | (20.21) | (33.07) | (29.88) | (8.41) | (19.96) |
| Cladocerans | 472 | 489 | 1007 | 648 | 967 | 1008 | 1457 | 327 | 958 | 266 | 327 |
| | (.62) | (.61) | (1.12) | (.71) | (1.09) | (1.08) | (1.60) | (.36) | (1.07) | (.26) | (.38) |
| Other Crustaceans | 161 | 78 | 44 | 15 | 19 | 6 | 13 | 5 | 11 | .... | 4 |
| | (1.40) | (.50) | (.30) | (.07) | (.06) | (.09) | (.01) | (<.01) | (<.01) | .... | (<.01) |
| Chaetognaths | 541 | 418 | 267 | 229 | 103 | 139 | 66 | 124 | 62 | 2 | 17 |
| | (2.66) | (1.42) | (1.05) | (.68) | (.43) | (.53) | (.23) | (.45) | (.23) | (<.01) | (.03) |
| Appendicularians | 2138 | 1935 | 3170 | 3325 | 3708 | 3537 | 3729 | 3782 | 3999 | 1933 | 3673 |
| | (3.81) | (2.89) | (4.62) | (4.87) | (4.88) | (4.51) | (4.70) | (3.70) | (4.40) | (2.25) | (4.85) |
| Thaliaceans | 23 | 15 | 9 | 1 | 3 | .... | .... | .... | .... | .... | .... |
| | (.35) | (.11) | (.10) | (<.01) | (.02) | .... | .... | .... | .... | .... | .... |
| Larvae | 4871 | 3486 | 6922 | 3907 | 5127 | 6416 | 3048 | 12205 | 2623 | 975 | 890 |
| | (13.59) | (9.52) | (17.46) | (9.51) | (12.92) | (15.81) | (7.75) | (24.01) | (6.94) | (1.69) | (2.23) |
| Total Zoop. no./$m^3$ | 31099 | 39170 | 44272 | 44947 | 45841 | 44877 | 38747 | 62897 | 39583 | 21944 | 27867 |
| Total Zoop. dry wt($mg/m^3$) | (49.40) | (44.33) | (55.15) | (41.69) | (46.31) | (46.96) | (35.81) | (63.39) | (43.71) | (14.88) | (28.65) |

TABLE 14

Seasonal distribution of the major zooplankton groups in the St. Andrew Bay System (averages of all stations). Upper numbers in each row represent individuals/$m^3$; lower numbers in parentheses represent dry weight mg/$m^3$).

| | Aug. 59 | Nov. | Feb. 60 | June | July 61 | Aug. | Sept. | Oct. | Nov. | Dec. | Jan. 62 | Feb. | Mar. | April | May | June | Avg. 1961–62 | Percent Total Zoop. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dinoflagellates | .... | 9 | 4 | . .. | .... | .... | .. . | .... | .. . | .... | .... | 10553 | 22882 | 6 | 2 | 2 | 2787 | 6.94 |
| | .... | .... | . .. | .... | .... | .... | .... | .... | .... | .. . | .... | (3.91) | (8.47) | (<.01) | (<.01) | (<.01) | (1.03) | (2.41) |
| Tintinnids | 708 | 352 | 60 | 819 | 790 | 1163 | 977 | 354 | 57 | 42 | 13399 | 24 | 743 | 154 | 70 | 16309 | 2840 | 7.08 |
| | . .. | .... | .... | .... | (.01) | (.02) | (.01) | (<.01) | (.01) | (<.01) | (.29) | (<.01) | (.01) | (<.01) | (<.01) | (.39) | (.06) | (.15) |
| Hydromedusae | 27 | 8 | 39 | 36 | 11 | 58 | 131 | 115 | 160 | 30 | 17 | 7 | 5 | 11 | 109 | 122 | 65 | .16 |
| | .... | .... | .... | . .. | (.10) | (.22) | (1.02) | (.28) | (.28) | (.07) | (.11) | (.03) | (.01) | (.03) | (.65) | (.86) | (.30) | (.71) |
| Siphonophores | 18 | . . | 4 | .... | .... | 5 | 3 | 3 | 5 | 4 | 5 | 2 | 1 | 2 | 16 | 12 | 5 | .01 |
| | .. . | .... | .... | .... | .... | (.01) | (.01) | (.01) | (.01) | (.01) | (.01) | (<.01) | (<.01) | (.01) | (.04) | (.03) | (.02) | (.04) |
| Rotifers | .... | 254 | 39 | .... | .... | .... | .. . | 5 | 267 | 3280 | 19551 | 12 | 7 | 8 | 154 | 780 | 2005 | 4.99 |
| | .... | .... | .... | .... | .... | .... | .... | .... | (.06) | (.79) | (4.62) | (<.01) | (<.01) | (<.01) | (.02) | .... | (.46) | (1.07) |
| Molluscs & Polychaetes | 17 | .... | .... | 69 | 21 | 10 | 5 | 15 | 2 | 6 | 3 | .... | 1 | 411 | 25 | 7 | 42 | .10 |
| | .... | .... | .... | .... | (.03) | (.01) | (.01) | (.02) | (<.01) | (.01) | (<.01) | .... | (<.01) | (.52) | (.03) | (.05) | (.06) | (.13) |
| Copepods | 7440 | 21194 | 12848 | 27851 | 18053 | 40959 | 31574 | 29811 | 24719 | 13287 | 22377 | 3444 | 11054 | 8111 | 28254 | 52726 | 23697 | 59.03 |
| | .... | .... | .... | .... | (19.47) | (35.87) | (37.39) | (33.60) | (24.79) | (16.15) | (31.98) | (3.62) | (12.21) | (8.99) | (29.59) | (32.58) | (23.85) | (55.82) |
| Cladocerans | 427 | 48 | 340 | 840 | 660 | 2210 | 872 | 471 | 221 | 100 | 1812 | 120 | 887 | 289 | 796 | 207 | 720 | 1.79 |
| | .. . | .... | .... | .... | (.80) | (2.71) | (1.16) | (.61) | (.31) | (.10) | (1.67) | (.11) | (.82) | (.27) | (.88) | (.29) | (.81) | (1.89) |
| Other Crustaceans | 16 | 2 | 131 | 7 | 5 | 64 | 29 | 42 | 40 | 40 | 10 | 1 | 4 | 2 | 22 | 84 | 32 | .08 |
| | .... | .... | .... | .... | (.32) | (.79) | (.35) | (.25) | (.12) | (.09) | (.03) | (<.01) | (.02) | (<.01) | (.05) | (.63) | (.22) | (.52) |
| Chaetognaths | 160 | 154 | 43 | 185 | 192 | 265 | 147 | 256 | 142 | 61 | 57 | 25 | 42 | 71 | 308 | 591 | 180 | .45 |
| | .... | . .. | .... | .... | (.63) | (.90) | (.74) | (.83) | (.49) | (.23) | (.64) | (.06) | (.44) | (.13) | (1.61) | (1.80) | (.71) | (1.66) |
| Appendicularians | 1571 | 991 | 168 | 3390 | 1623 | 6531 | 4359 | 3654 | 3928 | 3338 | 190 | 61 | 1553 | 2135 | 5764 | 4949 | 3173 | 7.90 |
| | .... | .... | .... | .... | (1.60) | (8.30) | (6.56) | (5.01) | (5.44) | (5.00) | (.41) | (.07) | (2.95) | (3.06) | (7.17) | (4.00) | (4.13) | (9.67) |
| Thaliaceans | 5 | .... | .... | .... | 1 | 4 | 6 | 3 | 1 | .... | 4 | 5 | .... | .... | 21 | 14 | 5 | .01 |
| | .... | .... | .... | .... | (.02) | (.02) | (.05) | (.02) | (.01) | .... | (.07) | (.21) | .... | .... | (.18) | (.09) | (.05) | (.13) |
| Larvae | 1351 | 402 | 1633 | 3329 | 2007 | 5897 | 7521 | 2175 | 2603 | 1452 | 1393 | 261 | 2207 | 1746 | 6153 | 21668 | 4590 | 11.43 |
| | .... | .... | .... | .... | (5.52) | (16.58) | (20.88) | (6.13) | (6.48) | (3.64) | (4.08) | (.59) | (5.69) | (4.49) | (17.75) | (40.49) | (11.03) | (25.80) |
| Total Zoop. no./$m^3$ | 12740 | 23414 | 15319 | 36526 | 23363 | 57166 | 45624 | 36895 | 32145 | 21640 | 58818 | 14515 | 39386 | 12694 | 41694 | 97471 | 40141 | |
| Total Zoop. dry wt(mg/$m^3$) | .... | .... | .... | .... | (28.51) | (65.42) | (68.16) | (46.74) | (38.08) | (26.08) | (43.90) | (8.60) | (30.62) | (17.50) | (57.96) | (81.20) | (42.73) | |

The variety of organisms seen in plankton sample aliquots decreased with decreasing salinity in a fairly linear manner (Fig. 5). Greatest plankton variety occurred at S3 (43 types/aliquot) and S2 (41 types/aliquot), stations with the highest mean salinities, and the least variety occurred at N1 (14 types/aliquot) and E1 (18 types/aliquot), stations with the lowest salinity averages. At E1 only five species exceeded 1% of both the zooplankton number and dry weight and the dominance of *Acartia* was pronounced. At this station *Acartia* accounted for 63% and 46% of the zooplankton number and dry weight respectively. At S3, where plankton diversity was greatest, 12 species averaged greater than 1% of the population number and weight with the most abundant species, *Paracalanus crassirostris*, accounting for only 18% of the zooplankton number and 11% of the weight.

Without regard to species composition, both total numbers and biomass were rather evenly distributed throughout the bay complex, though unusually high averages were obtained for W1 at the head of West Bay (62,900/$m^3$; 63.4 mg/$m^3$) and comparatively low mean values were recorded for N1 (21,900/$m^3$; 14.9 mg/$m^3$) and E1 (27,900/$m^3$; 28.6 mg/$m^3$) in the upper reaches of North and East Bays. The average for all stations for 1961–62 was 40,100 plankters/$m^3$ and 42.7 mg of zooplankton dry weight/$m^3$.

Zooplankton seasonal data reveal that in 1961–62 biomass and numerical fluctuations were rather closely associated. In late summer of 1961 a zooplankton numerical maximum appeared in August and a biomass peak occurred a month later in September.

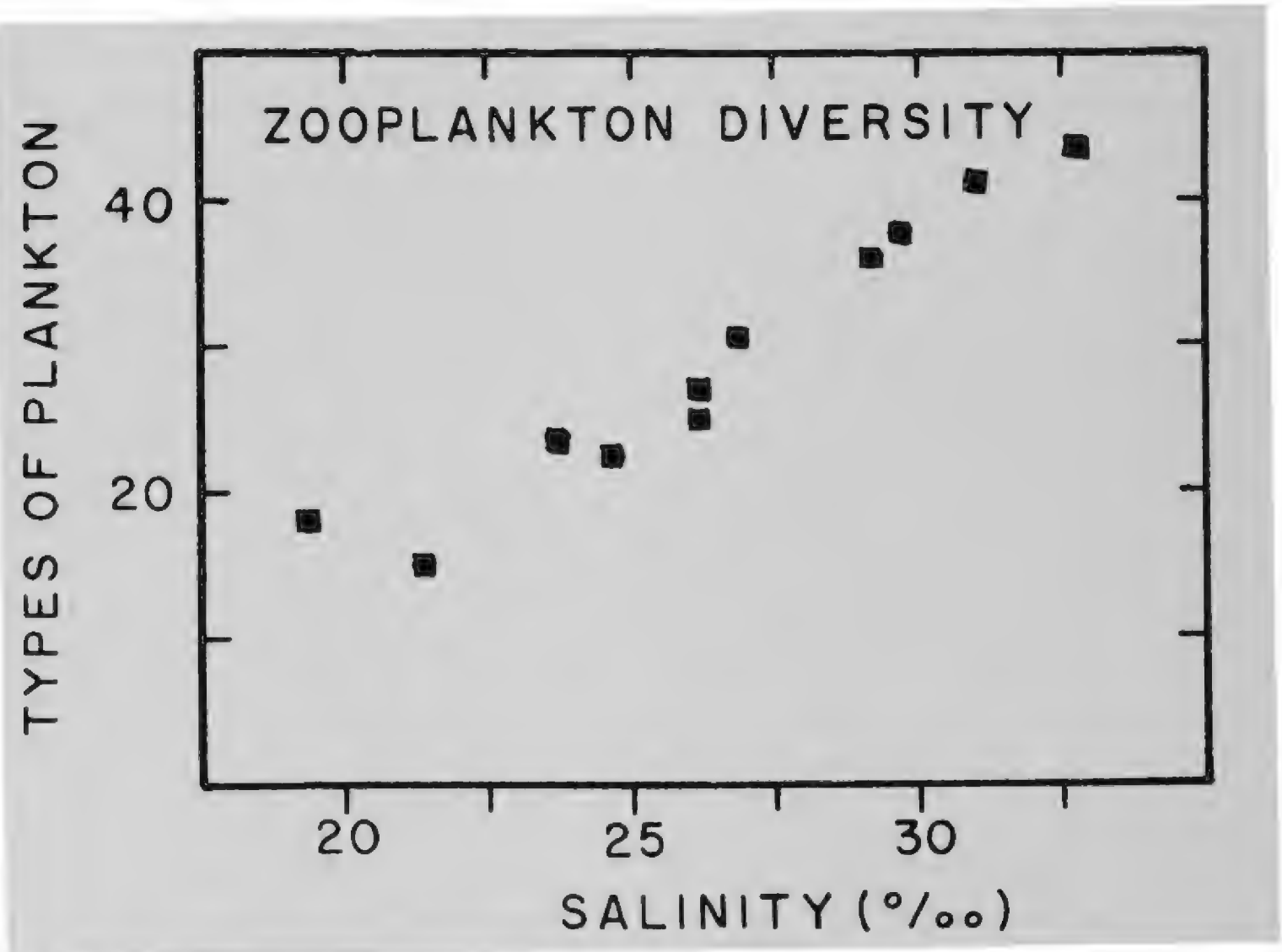


FIG. 5. Distribution (1961–62) of zooplankton species diversity in the St. Andrew Bay System with respect to salinity.

Biomass and numerical fluctuations for the remainder of the year corresponded in time. There was a moderate peak in January, a smaller one in March, and the annual maximum in June. Minima were recorded for July, December, February, and April. In 1959–60 zooplankton counts were largest in November and June while lowest counts were obtained for August and February.

Zooplankton variety (Fig. 6) was greatest during the warmer months and maxima were recorded for September 1961 (34 types/aliquot) and June 1962 (37 types/aliquot). Faunal variety was comparatively low from February through April with the minimum occurring in February 1962 (16 types/aliquot).

Peaks in zooplankton numbers in the warmer months of 1961–62 (Table 14) can be attributed to copepods and to a lesser extent to larvae, appendicularians and tintinnids. In January, tintinnids and rotifers as well as copepods contributed significantly to the winter numerical peak. The minimum in December resulted primarily from a drop in the copepod population and that for February, the minimum of the year, was due to the comparative scarcity of nearly all types of plankton except *Noctiluca*. Virtual disappearance of *Noctiluca* along with continued scarcity of other plankters accounts for the small standing crop of April.

Biomass peaks (Fig. 4 H) in the warmer months were formed predominantly by copepods and invertebrate larvae. Copepods, again, were largely responsible for the January biomass pulse while a small increase in copepods and a doubling of the *Noctiluca* population caused the much smaller peak which followed in March. Though tintinnids and rotifers were abundant in January, they did not contribute a proportional amount to the zooplankton biomass.

Even though data for the 1959–60 quarterly survey are not as complete as are those for the 1961–62 monthly investigation, it is probably safe to state on the basis of these two surveys, that standing crop level varies from year to year (Fig. 7) and that peaks do not necessarily correspond in time from one year to the next. Poor agreement of yearly plankton cycles also has been noted in other estuaries (e.g. Sheepscot estuary: Stickney, 1959; Delaware Bay: Deevey, 1960) and in coastal waters (Cape Cod to Chesapeake Bay: Bigelow and Sears, 1939).

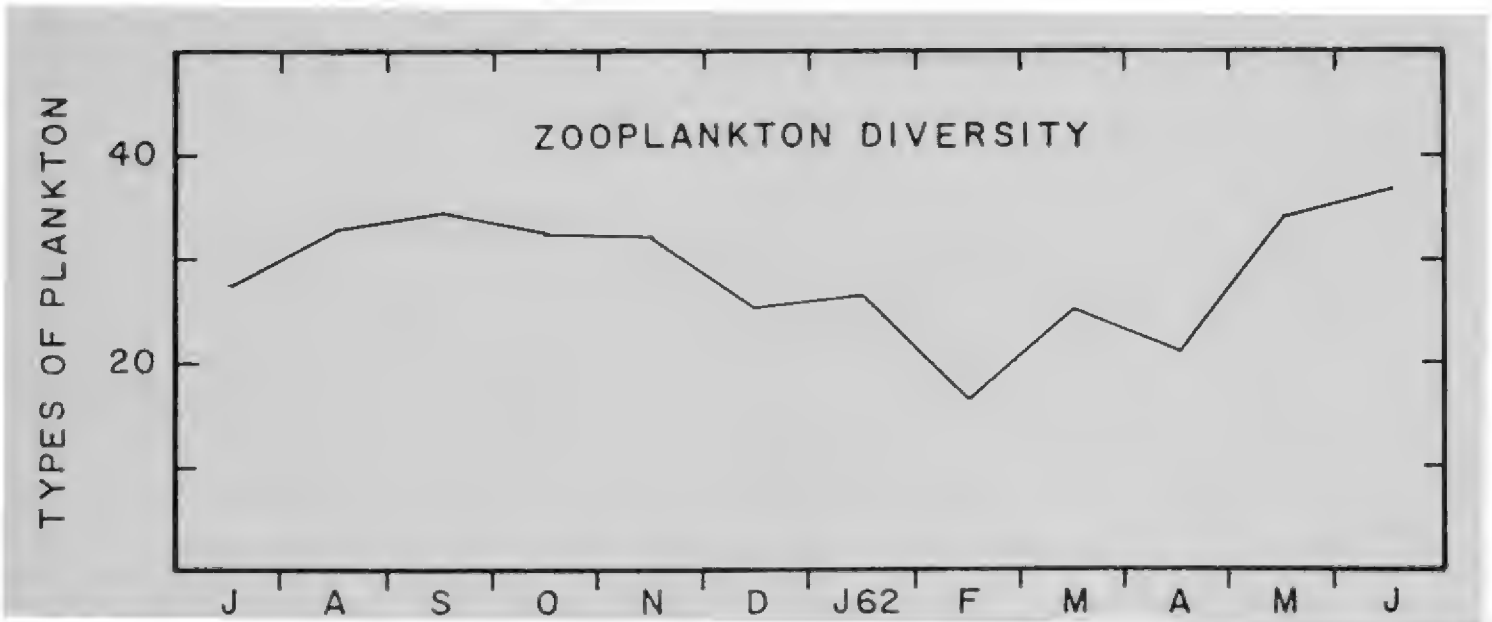


FIG. 6. Seasonal (1961–62) distribution of zooplankton species diversity in the St. Andrew Bay System.

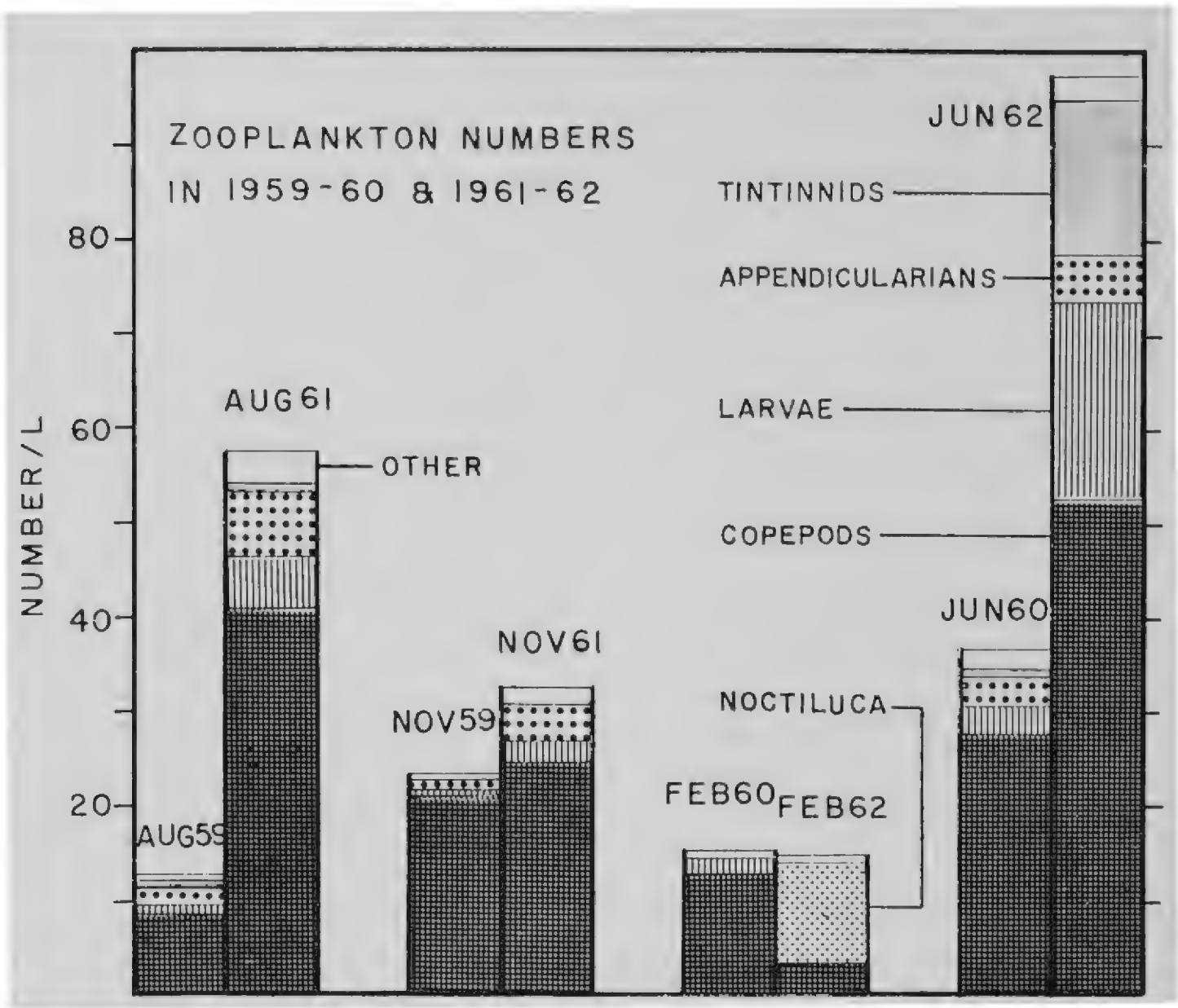


FIG. 7. Zooplankton standing crop in the St. Andrew Bay System in two different years (1959–60, 1961–62).

## Discussion of Results

### FACTORS INFLUENCING THE DISTRIBUTION OF PLANKTON BIOMASS

Multiple linear regression analyses have been used to evaluate relationships between diatom standing crop and salinity and temperature. Possible delayed effects (one month) of salinity and temperature on diatom biomass have been included in the analyses. Results of these regression analyses are in Table 15.

TABLE 15

Multiple linear regression analyses of diatom volume, surface salinity, and temperature data (dependent variable: diatom volume; independent variables: temperature, salinity)

| Independent variable | Degrees of freedom | T-value of regression coefficient | Cumulated proportion of variance ($R^2$) |
|---|---|---|---|
| | Diatom data offset (lag) by one month | | |
| Temperature | 118 | 2.08[a] | 0.023 |
| Salinity | 118 | 3.15[b] | 0.076 |
| | No time lag of diatom data | | |
| Temperature | 129 | 1.81 | 0.012 |
| Salinity | 129 | 5.57[b] | 0.192 |

[a] Significant at t.05.
[b] Significant at t.01.

In both the month-lag and non-lag analyses salinity accounts for a significant portion (at t.01) of the diatom biomass variance. The strongest t-test is obtained for the non-lag regression which may indicate that salinity lag effects are better measured by a time interval other than one month. The temperature-diatom biomass relationship is not strong and is significant only at t.05 in the month-lag analysis. Cumulated proportion of variance figures indicate that at best about 20% of the diatom biomass variability can be attributed to the combined effects of salinity and temperature. While it may be that more intensive sampling would ultimately reveal lag intervals which would yield stronger statistical relationships between diatom biomass and the two hydrographic parameters, it is also probable that a good portion of the unaccounted diatom volume variance was caused by variables not assayed. To date there is no information on primary production, grazing rates, dissolved nutrients, or the effects of circulation patterns on the diatom population in the St. Andrew Bay System. This information is necessary before the most important regulators of the diatom population can be determined.

Multiple linear regression analyses also have been used to investigate the extent that diatom biomass, salinity, and temperature influenced variations in zooplankton biomass (Table 16). As in the previous analyses, delayed effects of the independent variables were studied. The temperature-zooplankton biomass regression coefficient is significant (t.01) in both the time-lag and non-lag studies with the t-test being strongest in the lag analysis. Salinity, on the other hand, is not linearly related to zooplankton biomass to a statistically significant degree.

Diatom biomass accounts for a significant portion of zooplankton biomass variance only in the non-lag analysis. Cumulated proportion of variance figures show that diatom standing crop fluctuations account for only 11.5% of the zooplankton biomass variance. Perhaps a stronger relationship would be expected if other possible sources of zooplankton food, such as detritus, flagellates, micro-organisms, and even organically rich bottom sediments, were not available.

The food value of detritus to higher forms of zooplankton has been questioned in the past (Riley, 1959), but Riley (1963) recently suggested that detritus formed by the adsorption of dissolved organic matter on particle or bubble surface forms a rich supply of supplementary food in coastal waters. In fact, Baylor and Sutcliffe (1963) have successfully reared *Artemia* on detritus formed by bubbling air through a medium rich in dissolved organic substances. Also Cowey and Corner (1963) have demonstrated that total

TABLE 16

Multiple linear regression analyses of zooplankton biomass (dry weight) and diatom volume, temperature, and salinity data (dependent variable: zooplankton biomass—dry weight; independent variables: diatom volume, temperature, and salinity)

| Independent variable | Degrees of freedom | T-value of regression coefficient | Cumulated proportion of variance ($R^2$) |
|---|---|---|---|
| Zooplankton biomas data offset (lag) by one month | | | |
| Diatom volume | 117 | —0.35 | 0.004 |
| Temperature | 117 | 5.91[a] | 0.210 |
| Salinity | 117 | 1.91 | 0.024 |
| No time lag of zooplankton data | | | |
| Diatom volume | 128 | 3.09[a] | 0.115 |
| Temperature | 128 | 3.46[a] | 0.071 |
| Salinity | 128 | 0.97 | 0.006 |

[a] Significant at t.01

particulate matter in waters off Plymouth is little different from the diatom *Skeletonema costatum* in the variety and quantiy of its amino acids. Flagellates are a likely source of nutrition since copepods and various invertebrate larvae thrive on this diet in the laboratory (Loosanoff *et al.*, 1957). Too, Manuilova (1957, 1958) has found that some species of fresh water cladocerans, at least, can grow and reproduce using bacteria as the sole constituent of the diet. Although there are little data on the significance of organically rich bottom sediments as zooplankton food, this possibility cannot be discounted. If any of the above alternate food sources are utilized by zooplankton it might have the effect of reducing grazing on the diatom population.

Cumulated proportion of variance values in Table 16 indicate that temperature, salinity, and diatom biomass together account for only a small portion of the total variance of zooplankton biomass, even when lag effects are considered. This suggests, as in the case of diatom variation, that parameters not included in the statistical analyses were responsible for most of the observed variations. It is unfortunate that accurate quantitative records were not maintained on large plankters such as scyphomedusae and ctenophores for there is some evidence that they play an important role in the population dynamics of the St. Andrew estuaries. A rough estimate of their abundance is available, however, in the form of records of presence or absence of scyphomedusae and ctenophore fragments in sample aliquots. As shown in Table 17, fragments were found in samples collected at eight of the 11 stations during January and February 1962.

It is surmised that by February a considerable quantity of the zooplankton crop had been consumed, thus accounting for the February drop in biomass. By March scyphomedusae, primarily *Cyanea capillata* (Linnaeus), and ctenophores had almost disappeared. Zooplankton standing crop remained low through March and April which may be considered the lag time required for the microplankton population to attain pre-February levels.

Table 17 also shows that scyphomedusae (*Chrysaora quinquecirrha* [Desor]) and ctenophores were numerous in August 1959 and that ctenophores were again prevalent in February 1960. They occurred during the time when the least plankton was collected. It may be, as numerous authors have suggested (Nelson, 1925; Barlow, 1955; Conover,

TABLE 17

Occurrence of ctenophore and scyphomedusa fragments in sample aliquots

| Date | Fragment occurrence (fraction of samples examined) |
|---|---|
| Aug '59 | 6/8 |
| Nov '59 | 0/8 |
| Feb '60 | 6/8 |
| Jun '60 | 0/8 |
| Jul '61 | 3/11 |
| Aug '61 | 3/11 |
| Sept '61 | 1/11 |
| Oct '61 | 0/11 |
| Nov '61 | 1/11 |
| Dec '61 | 1/11 |
| Jan '62 | 8/11 |
| Feb '62 | 8/11 |
| Mar '62 | 1/11 |
| Apr '62 | 1/11 |
| May '62 | 1/11 |
| Jun '62 | 1/11 |

1961; Cronin *et al.*, 1962), that these large predators, which feed indiscriminately (Lebour, 1922; Mikhailov, 1962; Zenkevitch, 1963) on the rest of the community, make vast inroads on the microzooplankton of this bay complex. These predators, in fact, must be considered along with physical parameters such as salinity and temperature in interpreting seasonal fluctuations of estuarine zooplankton.

## COMPARISON OF STANDING CROP WITH THAT OF OTHER AREAS

A comparison of phytoplankton counts for the St. Andrew Bay complex with those for other areas in the Gulf of Mexico and along the Atlantic coast of North America is shown in Table 18. It appears that mean numbers of diatoms in St. Andrew Bay are somewhat smaller than the averages listed for other estuaries whereas they are considerably higher than the coastal and offshore means. Patten *et al.*'s (1963) value approaches the St. Andrew Bay figures, but since they recorded chains of cells as single units, their counts would tend to underestimate total cell numbers.

Dissolved nutrients in the St. Andrew Bay System were not investigated in the period of this survey but phytoplankton standing crop suggests that nutrient levels in the bay complex were not high compared to the other estuaries considered. The relatively low St. Andrew Bay cell densities are not typical of a nutrient rich domestically polluted environment and though primary and secondary treated domestic wastes enter the bay system in three places, stations nearest the outfalls (N1, N2, S1, E4) did not yield unusually high cell counts. Also, the St. Andrew Bay System does not receive extensive fresh water runoff. The principal sources, the Econfina River and the local bayous, drain nutrient poor soils which supports mostly scrub oak, pine, and palmetto. Conversely, phytoplankton inhibition by industrial wastes seems unlikely since the St. Andrew Bay area is not heavily industrialized. One of the largest possible sources of toxic effluent would be the International Paper Company on the north shore of East Bay, but station E4 which is directly opposite the plant demonstrated no anomalously low cell densities nor did other stations adjacent to E4. Perhaps the major source of phytoplankton nutrients

TABLE 18

A comparison of phytoplankton abundance in St. Andrew Bay with abundance in other areas in the Gulf of Mexico and the northwestern Atlantic

| Area | Source | Diatoms[a] ($10^5$ cells/1) | Sampling period |
|---|---|---|---|
| ESTUARIES | | | |
| St. Andrew Bay | Hopkins, 1964 | 8.46-s[b] | All seasons |
| Mississippi Delta | Thomas & Simmons, 1960 | 10.60 | Jan, Apr |
| | | 35.67-s | Fall, Feb, May |
| Lower Chesapeake Bay | Patten *et al.*, 1963 | 9.38-s | All seasons |
| Long Island Sound | Conover, 1956 | 24.30 | All seasons |
| Tisbury Pond | Hulburt, 1956 | 3.44-63.30 | All seasons |
| Narrangansett Bay | Pratt, 1959 | 53.06 | All seasons |
| COASTAL AND OFFSHORE WATERS | | | |
| Georges Bank | Sears, 1941 | 2.10 | Mar, Jun |
| Vineyard Sound | Lillick, 1937 | .25 | All seasons |
| Block Island Sound | Riley, 1952 | 3.25 | All seasons |
| Continental shelf | Hulburt, 1963 | .92-10m | All seasons |
| Bermuda to shelf | Hulburt, 1963 | .27-10m | May-Aug, Dec-Mar |
| Sargasso Sea | Riley, 1957 | .01-.03 | All seasons |

[a] Some averages include thecate dinoflagellates and silicoflagellates, however, diatoms constitute the bulk of the mean.
[b] Averages followed by s (surface) or 10m indicate that samples were taken only from these depths.

is the indrafted coastal water which composes the deeper layers of the bay system. If this indeed proves to be the case, it might explain why St. Andrew Bay cell counts fall between usual estuarine and offshore oceanic values.

The annual chlorophyll *a* average for St. Andrew Bay (Table 19) is also well below that of the other listed estuaries. It is greater, however, than the offshore values with the exception of those of Marshall (1956) and Riley (1941) for the West Coast of Florida and for Georges Bank respectively. Riley's figure represents total chlorophyll and Marshall's value is for November only.

An important factor to consider in these chlorophyll comparisons is that the St. Andrew Bay annual average was determined from surface samples whereas three of the five averages for other estuaries were derived from samples taken at more than one level in the water column.

Zooplankton standing crop data for Gulf of Mexico and Western Atlantic waters expressed in terms of numbers and dry organic weight per cubic meter of water are shown in Table 20. Dry weights in most cases have been computed from displacement volumes with the following conversion factor (Deevey, 1952):

$$\text{dry organic weight} = 0.089 \times \text{cc displacement volume.}$$

In regard to plankton numbers, the St. Andrew Bay average is less than the mean for Tisbury Pond (40,100 vs 52,200) and considerably less than the Long Island Sound average (40,100 vs 62,000). On the other hand the St. Andrew Bay average is significantly larger than the means for the five coastal and offshore areas listed (Tortugas, slope waters off Georgia, Sargasso Sea, slope waters off New Jersey, Block Island Sound). While the Grice and Hart (1962) values for Sargasso and slope waters off New Jersey perhaps would have been larger had they used nets finer than #6 mesh, it is unlikely that these averages would have approached those for St. Andrew Bay.

TABLE 19

A camparison of the chlorophyll a content of St. Andrew Bay waters with plant pigment concentrations in other areas of the Gulf of Mexico and the western Atlantic

| Area | Source | Chl. a (mg/m³) | Sampling period | Vertical salinity gradient ppt |
|---|---|---|---|---|
| ESTUARIES | | | | |
| St. Andrew Bay | Hopkins, 1964 | 2.13-s[b] | All seasons | 1.0–9.2 |
| | | 4.87 | Jan, Apr | 2.9–8.5 |
| Alligator Harbor | Marshall, 1956 | 4.3-s | All seasons | ~1.0 |
| Tampa Bay | Marshall, 1956 | 6.6-s | Sept, Jan | |
| Sapelo & Doboy | | | Apr-May | |
| Sounds | Ragotzkie, 1959 | 11.7 | Feb-May, Jul | Well mixed |
| Lower Chesapeake Bay | Patten *et al.*, 1963 | 6.15 | All seasons | 1.1–4.5 |
| Long Island Sound | Conover, 1956 | 6.14 | All seasons | ~1.0 |
| COASTAL AND OFFSHORE WATERS | | | | |
| Sargasso Sea | Ryther *et al.*, 1961 | .18 | Apr | |
| Florida Straits | Alexander & Corcoran, 1963 | .1-.3 | Jun | |
| Florida west coast[a] | Marshall, 1956 | 2.3-s | Nov | |
| Florida Keys | Marshall, 1956 | 1.2-s | Nov | |
| Dry Tortugas | Riley, 1939 | .33-s | Jul-Aug | |
| N.W. Atlantic | | | | |
| slope waters | Riley, 1939 | 2.1-s[c] | May Jun | |
| Georges Bank | Riley, 1941 | 3.6-s | ? | |

[a] Red tide values not included
[b] Surface samples
[c] All of Riley's values are for total plant pigments

TABLE 20

A comparison of zooplankton standing crop in St. Andrew Bay with abundance in other Gulf of Mexico and northwestern Atlantic waters

| Area | Source | #/m³ | Dry organic weight (mg/m³) | Net mesh | Comments |
|---|---|---|---|---|---|
| ESTUARIES | | | | | |
| St. Andrew Bay | Hopkins, 1964 | 40,100 | 33.1 | #10 | |
| Biscayne Bay | Woodmansee, 1958 | ..... | 53.4 | #6 | Surface |
| Lower Delaware Bay | Cronin *et al.*, 1962 | ..... | 31.2 | #2 | |
| Long Island Sound | Deevey, 1956 | 62,000 | 85.2 | #10 | |
| Tisbury Pond | Deevey, 1948 | 52,200 | .... | #10 | |
| Charlestown and Greenhill Ponds | Conover, 1961 | ..... | 59.6 | #12 | |
| Sheepscot Estuary | Stickney, 1959 | ..... | 36.5 | #2 | Jun-Nov |
| COASTAL AND OFFSHORE WATERS | | | | | |
| Tortugas | Riley, 1938 | 1,500 | .... | #20 | Surface |
| Continental shelf off North Carolina | St. John, 1958 | ..... | 24.6 | #2 | Jul-Aug Jan, Jun |
| Shelf waters—Cape Cod to Chesapeake Bay | Bigelow & Sears, 1939 | ..... | 35.6 | #2 | |
| Block Island Sound | Deevey, 1952 | 16,600 | 60.5 | #10 | |
| Vineyard Sound | (Clarke & Zinn, 1937) Deevey, 1952 | ..... | 26.6 | #2 | |
| Gulf of Maine | (Redfield, 1941) Deevey, 1952 | ..... | 26–47 | #0 | |
| Georges Bank | (Riley & Bumpus, 1946) Deevey, 1952 | ..... | 64.0 | #2 | |
| Slope waters off New Jersey | Grice & Hart, 1962 | 310 | 24.0 | #6 | Upper 200 m |
| Slope waters off Georgia | Riley, 1939 | 900 | 4.0 | #10 | May-Jun, upper 300 m |
| Sargasso Sea | Grice & Hart, 1962 | 71 | 1.8 | #6 | Upper 200 m |

The dry organic weight figure for St. Andrew Bay is substantially smaller than averages of the other listed estuaries with the exception of lower Delaware Bay and the Sheepscot estuary. Sampling in the Sheepscot and Delaware estuaries was with nets of #2 mesh, a mesh shown by Deevey (1952) to fish poorly for the small plankters which predominate in estuaries. It is possible, then, biomass averages for these two estuaries also would have exceeded the St. Andrew Bay mean had finer nets been employed.

St. Andrew Bay biomass, instead of approximating standing crop of the estuaries, falls more within the range of the values listed for coastal and offshore waters. Georges Bank and Block Island Sound averages, however, are noticeably higher than the St. Andrew Bay dry weight average, whereas Sargasso Sea and Georgia slope water biomass levels are significantly lower. Comparison here, as above, is of catches made with nets of various meshes.

Zooplankton population density and biomass values for St. Andrew Bay were based on the 12 month 1961–62 survey. During this year it appears that scyphomedusa and ctenophore predation was heavy. The effects of this predation were apparent from February through April, a period when the reproductive potential of the community is probably at its lowest level of the year. Had predation been less severe perhaps St. Andrew Bay annual standing crop averages would have approached more closely those of the other estuaries considered. Whether or not 1961–62 was anomalous with regard to scyphomedusa and ctenophore consumption of microzooplankton can be determined only with a long term sampling program.

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# Studies on bivalve molluscs of the genus *Crassinella* in the Northwestern Gulf of Mexico: anatomy, ecology and systematics

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## Abstract

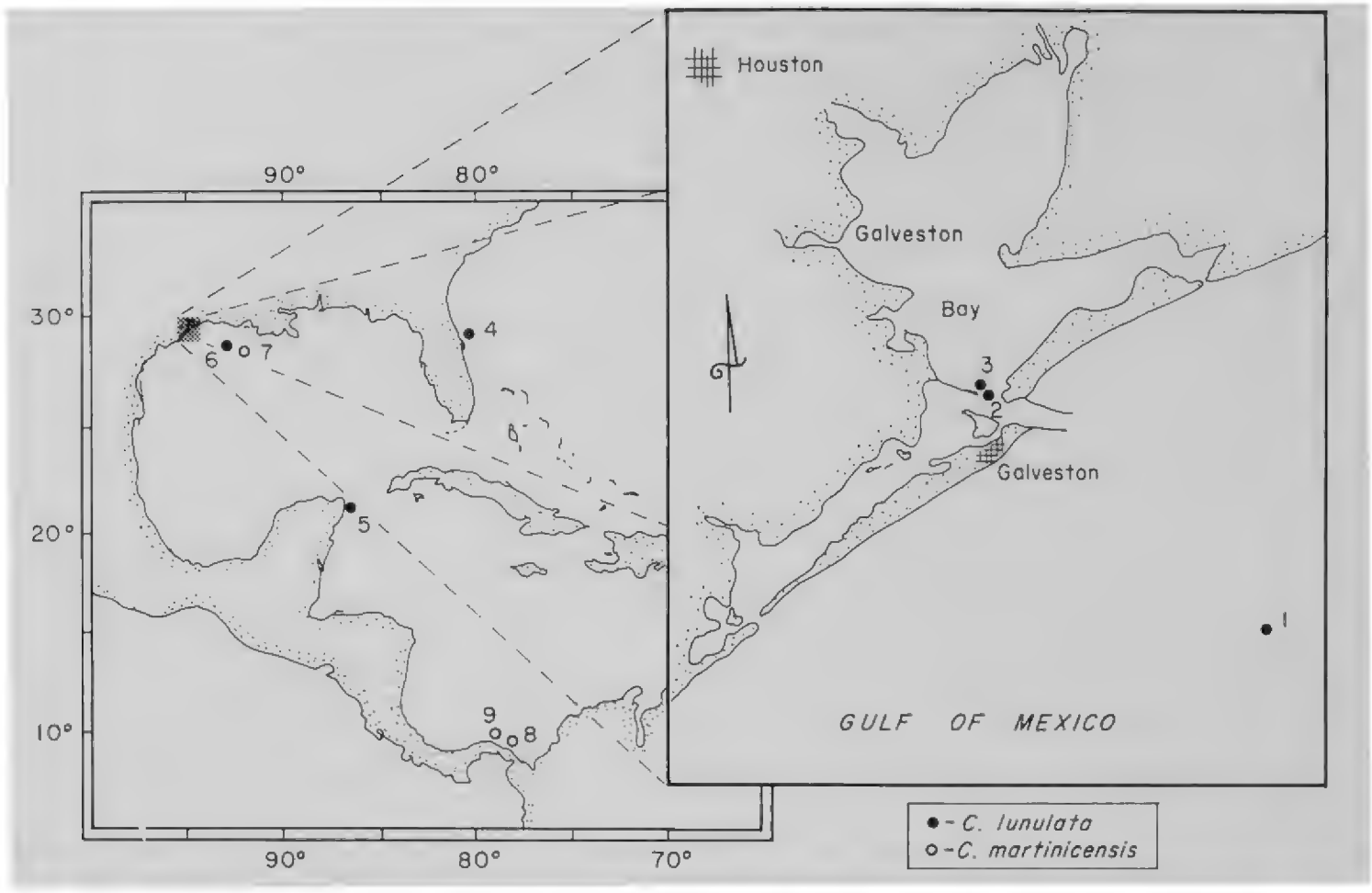
Nine nominal species of the genus *Crassinella* have been described in the Western Atlantic, but only two biological species are thought to exist there. The variations in size, shape, color and sculpture of these two species are discussed. *Crassinella lunulata* (Conrad) ranges from Cape Cod to the Gulf of Mexico, Antilles and possibly to Brazil. *C. martiniquensis* (d'Orbigny) is known only from the Caribbean and Gulf of Mexico. Little is known of the ecology of the latter species, reported from only three stations, at depths of 18 to 25 fathoms, from muddy bottoms, where coarser particles are sparse. *C. lunulata* is found mostly offshore at depths of one to 35 fathoms, and also in deeper passes in the bays along the coast of the Northwestern Gulf of Mexico. It is usually found where shell bottom predominates, with little mud.

A study of the anatomy of *C. lunulata* shows that there is only a single mantle suture, between the two siphonal areas; a single eulamelle-branchian demibranch on each side. The kidney contains granules which seem to increase in size with the size of the animal, and these are thought to be retained secretion products. The red color of the blood is thought to be hemaglobin, free in the plasma. This pigment is also described as contained in cells of the mantle, and in the cytoplasm of the eggs. A peculiar mantle gland, previously unreported, is present in *C. lunulata* and *Crassatella speciosa* (A. Adams) and may be characteristic of the family. A few early embryos found in the gills of these two species suggest they brood the early developmental stages, at least. The anatomy of *Crassinella lunulata* differs from that of *Crassatella speciosa* in several important respects, which are thought to represent generic rather than familial differences.

## Introduction

Bivalve molluscs of the genus *Crassinella* Guppy (1874) are presently known only from the temperate and tropical regions of the Atlantic and Pacific shores of the American continents. Their small size and great variability of shell characters, together with the facts that they occur in localized colonies and are rarely abundant, has led to a superfluous number of nominal species. Taxonomically there are several other important questions outstanding, such as whether *Crassinella* is sufficiently distinct from *Crassatella* to recognize it as a family, genus, or only subgenus of the latter. All three views have been held by various writers. There seems to be nothing previously written on the anatomy of this group, other than a few partial descriptions of the shell. Their ecology is poorly known, and several synecological studies which include members of this genus need to be collated.

The present study resulted from finding two colonies of *Crassinella lunulata* (Conrad 1834) at Galveston, Texas, in which live specimens could be obtained, and from having available several lots of comparative material from the northwest Gulf of Mexico porvided by the U.S. Fish and Wildlife Service at Galveston, as well as material collected by me while aboard the Research Vessel Anton Bruun along the east coast of Florida, off Yucatan, and the Caribbean side of Panama in September 1965 (see map and localities listed in Table 1).




Map showing the location of *Crassinella* examined in the present study. Station numbers correspond to those of Table 1.

TABLE 1

Localities and measurements of *Crassinella* populations studied.

| Locality reference | Number of specimens | Terminal Modal Height, mm. | Average Height, mm. | Range of Height, mm. |
|---|---|---|---|---|
| *C. lunulata* | | | | |
| 1 | 98(45) | 6.89 | 6.32 | 4.03–8.06 |
| 1a | 186(80) | 6.56 | 4.94 | 1.44–7.93 |
| 2 | 59(14) | 5.30 | 4.73 | 1.95–5.98 |
| 2a | 37(4) | 5.47 | 5.34 | 3.64–6.63 |
| 3 | 40(0) | 5.38 | 5.40 | 3.77–6.89 |
| 4 | 17(9) | 4.32 | 3.78 | 2.21–5.46 |
| 5 | 7(3) | 2.21 | 2.19 | 1.69–2.47 |
| 6 | 12(0) | 1.77 | 1.89 | 0.78–3.12 |
| *C. martinicensis* | | | | |
| 7 | 16(4) | 1.12 | 1.17 | 0.91–1.56 |
| 8 | 59(0) | 1.69 | 1.19 | 0.91–2.76 |
| 9 | 19(0) | 1.80 | 1.55 | 0.65–2.21 |

Explanation of Table 1

1. Heald Bank, 50 miles S.E. of Galveston, Texas (29° 8′ N. Lat., 94° 10′ W. Long.) 5 Fms. 30 June 1965.
1a. Same, Collected 31 October 1965.
2. Lower Galveston Bay, Texas. Intersection of Houston ship-channel and Intracoastal Canal. 42 feet deep. 10 August 1965.
2a. Same as 2, collected 29 October 1965.
3. Lower Galveston Bay, Texas. East of lower end of Texas City Jetty, 10 feet deep.
4. Off False Cape, east coast of Florida, (28° 41′ N. Lat., 80° 14.5′ W. Long.) 18–20 Fms. R/V Anton Bruun. 5 September 1965.
5. Off east coast of Yucatan 21° 41′ N. Lat., 86° 33.5′ W. Long.), 35 Fms. R/V Anton Bruun.
6. Northwestern Gulf of Mexico about 100 miles S.E. of Galveston, Texas (28° 46′ N. Lat., 93° 20′ W. Long.) 15 Fms.
7. Northwestern Gulf of Mexico about 100 miles S.W. of Marsh Island, Louisiana (28° 32′ N. Lat., 92° 20′ W. Long.) 25 Fms. Bottom of soft blue-grey mud.
8. North shore of Panama, (9° 36.2′ N. Lat., 79° 40.7′ W. Long.) R/V Anton Bruun. 23 Fms.
9. Gulf of San Blas, North side of Panama, between Islas de la Mulatas and the Isthmus (9° 37′ N. Lat., 78° 50′ W. Long.). 18 Fms. Fine blue-grey mud bottom. R/V Anton Bruun.
The figures in parentheses under "Number of specimens" are the number found alive, and included in the total number at left.

The cooperation of many persons of the U.S. Fish and Wildlife Service of Galveston is gratefully acknowledged, and particularly that of Messrs. Robert Temple, Cornelius Mock, and David Harrington. Dr. Edward Chin kindly provided the opportunity for the voyage aboard the R/V Anton Bruun. To Dr. H. B. Stenzel, I am grateful for several lots of comparative shell material and much advice regarding literature. I am indebted to the library of the U.S. National Museum and to the research library of the Shell Oil Company, Houston, for copies of several references. This work was also supported by the National Science Foundation on the R/V Anton Bruun as a part of the Southeastern Pacific Biological Oceanographic Program, and by NSF Grant GB-2753.

## Methods

From one to four liters of substrate sample, washed free of finer sediments, was picked over under a microscope to obtain the specimens at most of the stations listed in Table 1. For the three stations near Galveston over 50 liters were available at each sampling period (Table 1, stations 1, 1a, 2, 2a, 3). The shells obtained from station 6 of Table 1 were picked from a small amount of mud filling the cavities of larger shells.

Live specimens were studied from the two populations near Galveston. These were easily maintained for many weeks in the laboratory in a non-flowing, non-aerated aquarium. As these minute clams are difficult to open without tearing the tissues, the shells of preserved specimens were dissolved in 5% hydrocloric acid and 70% isopropyl alcohol. The cuticle was then picked off and specimens sectioned routinely, followed by hematoxylin and eosin stain. Whole mounts of deshelled specimens were prepared by staining in hematoxylin and destaining if necessary. Xylol was used as the clearing agent, after dehydration.

### Taxonomy of the Family and Genus

In January 1845, C. B. Adams published a new genus, *Thetis*, containing two new species of bivalves from Jamaica, *T. cerina* and *T. parva*, described in that order. He designated neither species as type of the genus, nor did he realize that the generic name was preoccupied, nor that *T. parva* had been previously named, nor that these species would on closer inspection prove to be members of two rather distantly related families, now termed Veneridae and Crassatellidae. Finding that *Thetis* had been used for a fossil venerid by J. Sowerby in 1826 (Min Conch. Tab. 513), Adams renamed his genus *Gouldia* in 1847, still without designating a type species. I have not seen the original papers by C. B. Adams, but depend on the quotations of his original works provided by Clench and Turner (1950), who have moreover published excellent photographs of the previously unfigured type specimens of his species.

In 1883 Dall validly designated *T. cerina* as the type of *Gouldia*, as noted by Keen (1938). Since *Gouldia cerina* is a member of the Veneridae, this removes that generic name from further attention in relation to the present problem, except to note that a number of older papers have applied *Gouldia* to the group of *T. parva*. They include two lists of the species of *Gouldia* (Tryon 1872; E. A. Smith 1881), and several papers on New England Mollusca (*e.g.*, Gould 1870; Verrill 1873). However, Stewart (1930) overlooked Dall's designation of the genotype. He recognized E. A. Smith's (1885) designation of *T. parva* as the first formal designation of the type of *Gouldia*. This matter

might be ignored, except that Stewart further thought *T. parva* sufficiently distinct from the Crassatellidae to separate it as a new family, which he consequently named Gouldiidae. Hence, we find a family based on a venerid, containing crassatellid species, in such subsequent useful but uncritical source books on mollusca of the east coast of North America as Johnson (1934), Perry (1940), and Pully (1952). For reasons to be given below, the genus *Crassinella* scarcely merits separation from the Crassatellidae. The name Gouldiidae should be dropped, at least in relation to this crassatellid group. We will not here enter the argument still raging about the validity of the genus *Crassatella*, accepting it in the usual broad sense in the present study (*see* Keen 1958).

In 1874 Guppy proposed the name *Crassinella* in a mere list of fossils of Trinidad, including a single species, "*martinicensis* d'Orb." This could have served as a new genus for any mollusc to which d'Orbigny had ever attached that trivial name. A year later he (Guppy 1875:42) noted that this was a replacement for *Gouldia* C. B. Adams, and that "the typical species are *C. pacifica* and *C. martinicensis*." For nomenclatorial purposes this merely tells us on which trivial name, *martinicensis* d'Orb., Guppy based the name *Crassinella*. The type of *Crassinella* is therefore determined by monotypy, *Crassatella martinicensis* d'Orbigny (1846), as Keen (1938) pointed out. Woodring (1925) argued that because *Crassinella* Guppy (1874) was proposed as a substitute for *Gouldia* C. B. Adams (1847) it must have the same type as a latter genus. This is unwarranted, because the genus *Crassinella* was originally (Guppy 1874) monotypic, and only in 1875 did Guppy note that it was a replacement for *Gouldia* Adams.

In seeking a proper generic name for the Crassatellid group of *T. parva*, Dall at first selected *Eriphyla* Gabb, the type of which is a Cretaceous fossil of California. He used this as a subgenus of *Crassatella* (Dall 1879; 1883a; 1889), preferring it to *Crassinella* because he vaguely remembered that *Crassinella* had been used by Conrad before Guppy used it, although he couldn't locate the Conradian reference (Dall 1879). Moreover, Dall (1881) provided a long and tortuous argument for why Gabb's name might apply. This led several people to use the name *Eriphyla* for species now recognized as *Crassinella*, *e.g.*, Harris (1895), and Singley (1893). Meanwhile, Fisher thought the group of *T. parva* was not of the same genus as *Eriphyla* Gabb, and since *Crassinella* Guppy might be preoccupied, he proposed the name *Pseuderiphyla* (Fisher 1887, type by monotypy, *C. martinicensis* d'Orbigny). Later, Dall (*in* Guppy and Dall 1897) also de-

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FIG. 1. Composite of internal anatomy of *C. lunulata*, based on live specimens and histosections. The right mantle lobe is cut away except for a small remnant in the siphonal region. *Apr*, anterior pedal retractor muscle; *Ec*, excurrent siphon; *G*, gill; *K*, kidney; *L*, liver; *Lp*, labial palp; *Mg*, marginal mantle gland; *P*, byssal groove along foot margin; *Ppr*, posterior pedal retractor; *R*, rectum, inside ventricle of the heart.

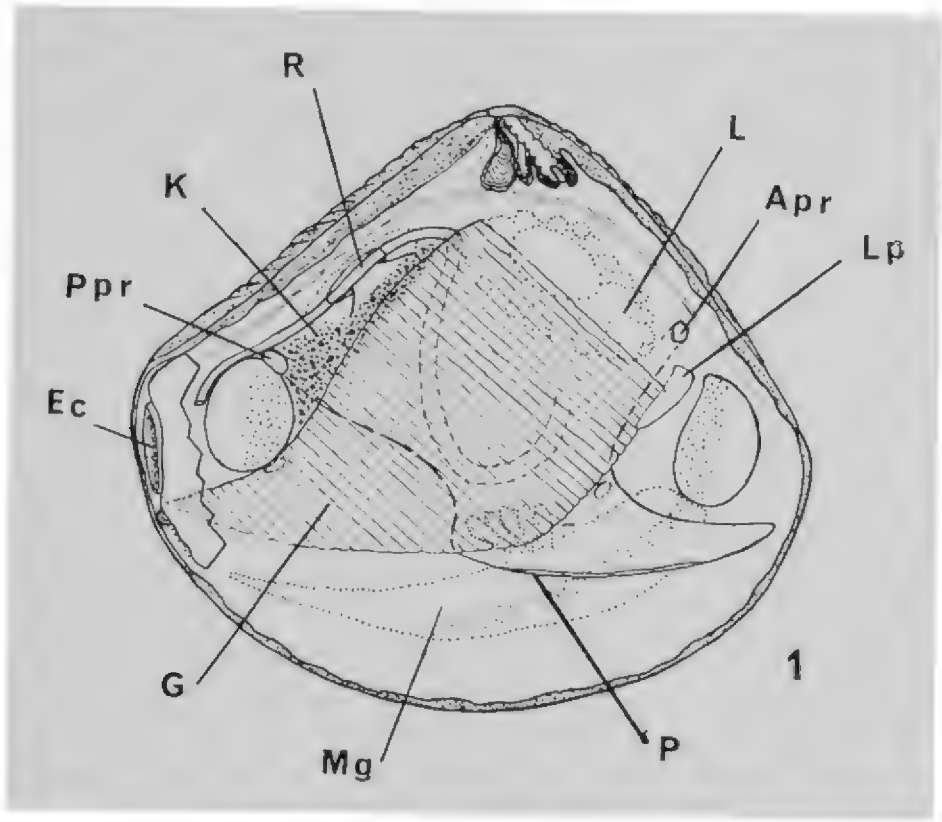
FIG. 2. Ovum (from gonad) and sperm (to same scale) of *C. lunulata* from Heald Bank, collected in October.

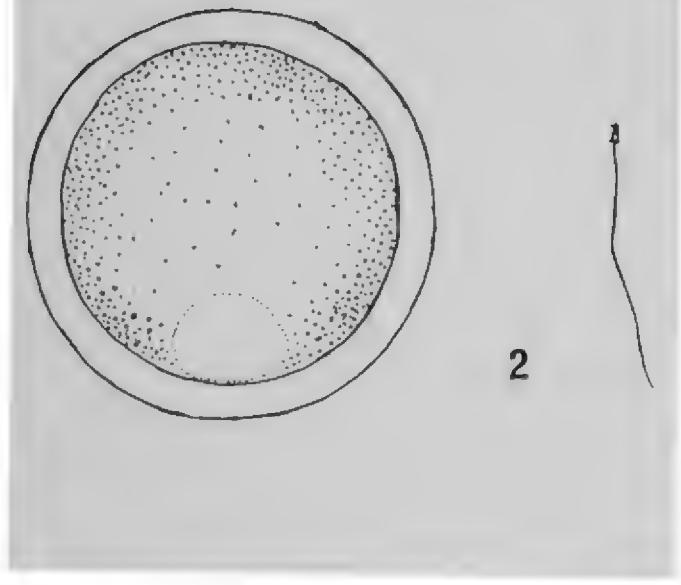
FIG. 3. Deshelled specimen of *C. lunulata* from off Florida, stained in hematoxylin and cleared to show the (right) testis (in black). The outline of the gills and labial palps are dashed lines.

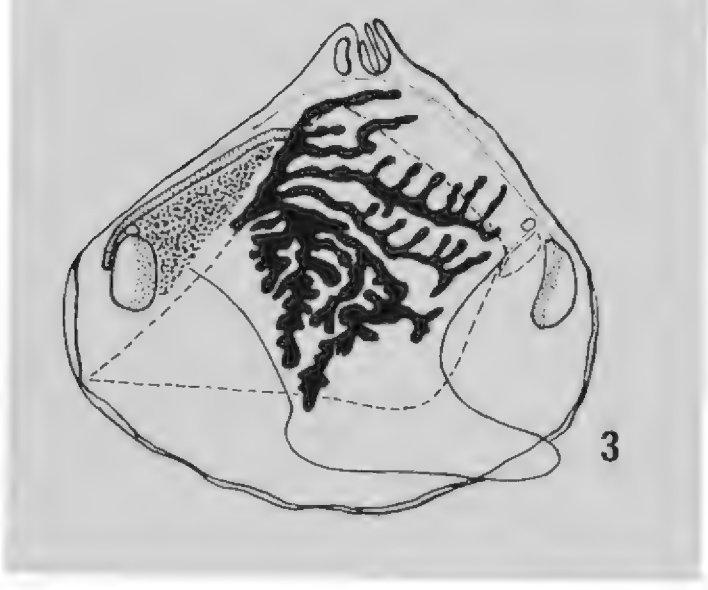
FIG. 4. Dorsal margin of the mantle of *C. lunulata*, from a live specimen. The hole in the lobe to the left allows contact of the two horns of the resilium; the densely stippled oval areas in the interdental papillae represent the location of hemaglobin within the tissues.

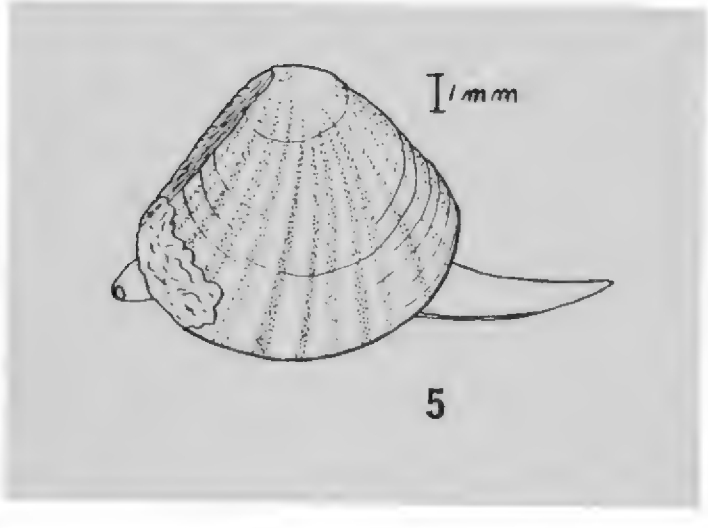
FIG. 5. Live specimen of *C. lunulata*, showing shape of extended siphon and foot. The posteroventral margin of the shell has a growth of calcareous algae. This specimen is the lower right one in FIG. 15.

cided *Eriphyla* Gabb could not be used for this group, and admitting that Conrad's use of *Crassinella* had never been found, he recognized *Crassinella* Guppy and pronounced *Pseuderiphyla* Fisher unnecessary.

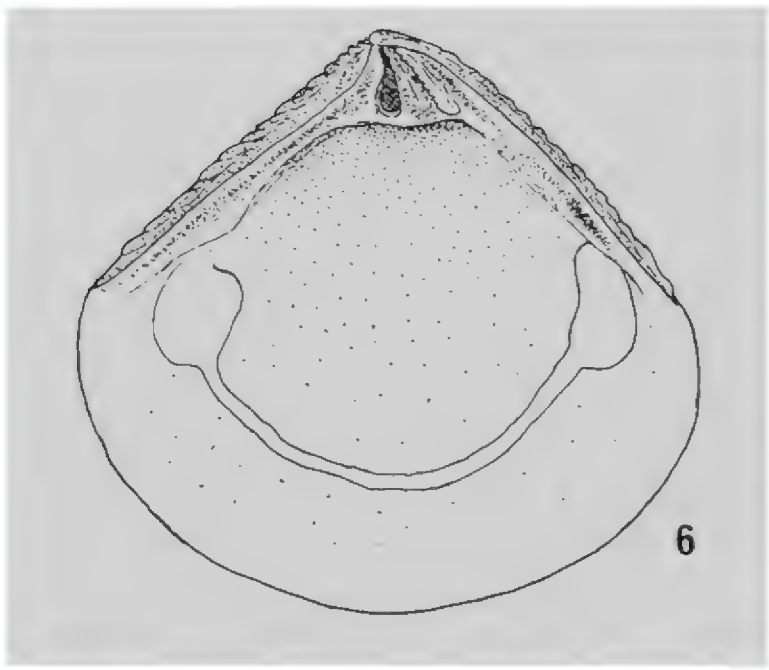


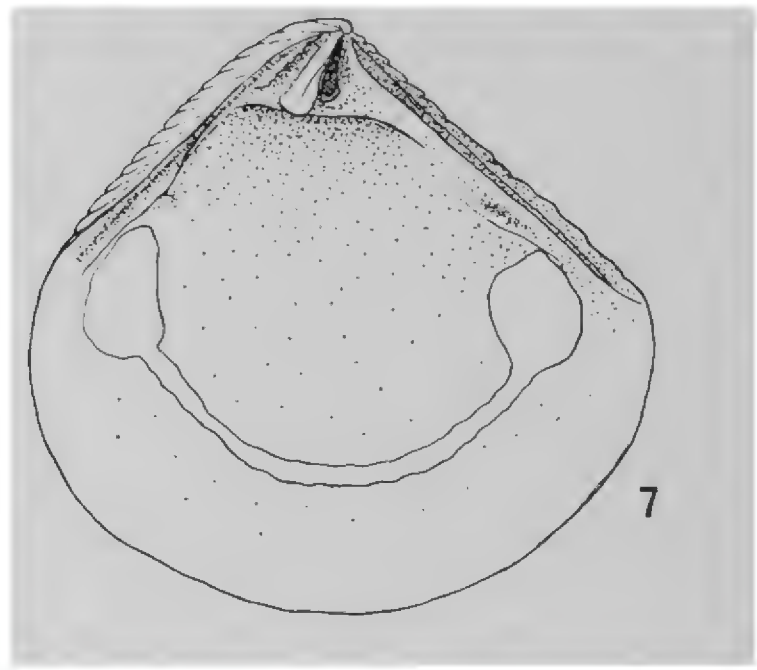



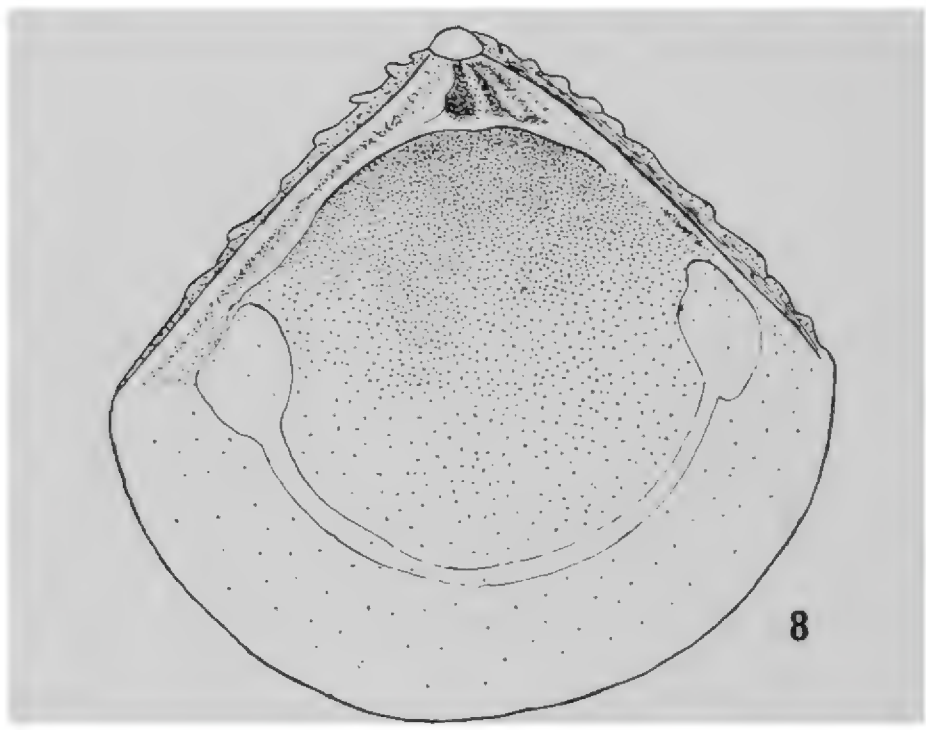



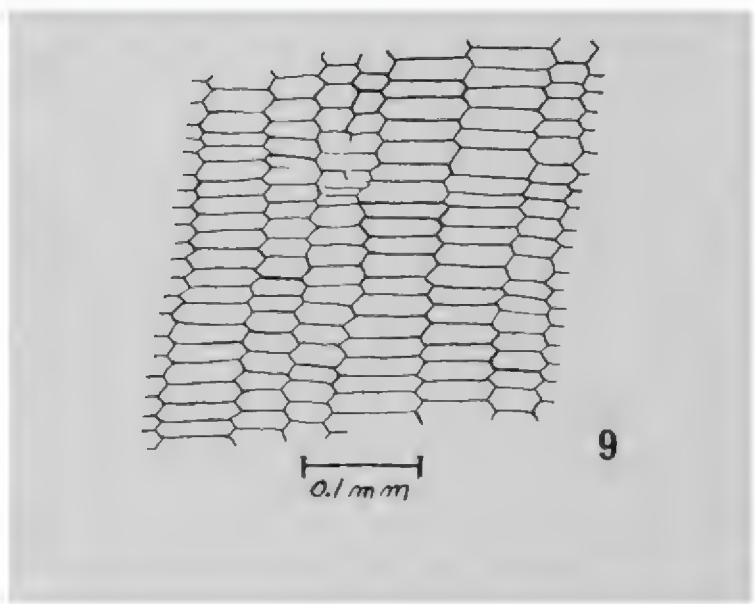


Descriptions of the species
*Crassinella lunulata* (Conrad 1834)
(Figs. 6, 7, 13, 15, 16, 17)



*Astarte lunulata* Conrad 1834, Jour. Acad. Nat. Sci. Philadelphia 7(1) :133. Not figured. Type locality: fossil in the Miocene of Suffolk, Virginia; 1840 Fossils of the Medial Tertiary of the U.S., p. 44, pl. 21 fig. 8 (not seen) ; 1862, Proc. Acad. Nat. Sci. Philadelphia 14:578 (as *Gouldia*).

*Thetis parva* C. B. Adams 1845 (January), Proc. Boston Soc. Nat. Hist. 2:9. Not figured. Type locality, Jamaica. A paratype is figured by Clench and Turner 1950, pl. 44, figs. 5, 6.

*Astarte mactracea* Linsley 1845 (April), Amer. Jour. Sci. 48(2) :275, name only and figure. Type locality: Stonington, Connecticut (in the stomach of a haddock). Gould 1848, Silliman's Jour. Sci. p. 233 (not seen) ; Gould 1870, Invertebrata of Mass., Ed. 2, p. 129.

*Crassatella guadalupenis* d'Oribgny 1846. Mollusques, *in* Sagra, Hist. . . Cuba, 2:289, Pl. 27, figs. 24–26. Type locality: Guadaloupe Island. This species is often dated 1853 (Keen 1938: 30), that on the title page of the volume in which it appeared. But d'Orbigny himself dated it 1846 on page 289, and the Catalogue of the Library of the British Museum of National History (p. 1780) notes that this part of Vol. 2 "probably appeared in 1883. The date 1846 appeared on p. 149 ff". E. A. Smith (1881) dated this species 1841, but apparently without justification.

*Astarte pfeifferi* Philippi 1848, Zeitschr. für Malak. p. 133. (original reference not seen; this nominal species is generally synonymized with the present species (Smith 1881; Lamy 1917). It was evidently not figured, and the type locality seems to be Cuba).

*Gouldia fastigiata* Gould 1862a, Proc. Bost. Soc. Nat. Hist. 8:282. Not figured. Type locality, "Frying-pan Shoals, North Carolina." 1862b, Otia Conchologica, p. 239.

*Eriphyla galvestonensis* Harris 1895, Bull. Amer. Paleont. 1(3) :8, Pl. 1, figs. 2a, 2b. Type locality: fossil, Artesian well, Galveston, Texas, 300 to 2,600 feet. According to his interpretation of these depths, p. 86, this would range from Miocene to Pleistocene. Dall 1903, Tert. Fauna Fla. 6:1478 pl. 49 fig. 14 [as *Crassatelites* (*Crassinella*) *galvestonensis*]

### *Shell*

The shell is small, subtriangular, strongly compressed, and equivalve. The umbones are minute, acute, midway the length of the shell, touching each other and strongly turned posteriorly (opistogyrous). The surface lateral to the umbo is more flattened than the rest of the valve. Valves are moderately thick for their size. The shape is very variable; the anterior and posterior dorsal margins form an angle at the umbones varying from slightly less to slightly more than 90°. These margins tend to be straight, or the posterior one concave, and the shape varies even between the two valves of the same shell, as noted below. The ventral margin is always strongly convex, forming almost a half circle.

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FIG. 6. Details of the left valve interior of *C. lunulata*. This specimen is photographed in FIG. 13.

FIG. 7. Details of the right valve of the shell of FIG. 6 (and FIG. 13).

FIG. 8. Interior of left valve of *C. martinicensis*, to show details of shell dentition. This shell is photographed in FIGS. 10 and 11.

FIG. 9. Details of the shell texture of *C. lunulata*, drawn at 450 × from a periostracum removed by acid digestion of the shell and mounted in balsam. Ventral margin of shell was toward top of the figure.

The lunule and escutcheon are well defined, extending from the umbones nearly to the anterior and posterior angles of the shell. Both have slightly concave surfaces which show only a few minute growth lines parallel to the shell margin. The periostracum in each is without any ornamentation. Both are slightly but regularly asymmetrical, and the asymmetry of one is a mirror image of the other.

The lunule is acutely pointed at both ends, more so at the umbones than at its front end. Its margins form gentle arcs which are most widely separated midway of their length. The left margin is an acute fold exactly along the anterior dorsal slope of the shell. The right margin of the lunule is slightly medial (*i.e.* toward the shell margin) to the anterior dorsal slope of its valve, and the anterior dorsal slope of the right valve is more rounded and always slightly higher than that of the left valve. In profile it always appears to be slightly more convex than the anterodorsal slope of the left valve, which is practically straight. Along the midline of the lunule, the margin of the left valve fits into a narrow marginal groove in the right valve, so that the margin itself of the left valve here constitutes the major lateral tooth, with a well defined socket in the opposite valve.

The escutcheon is much wider than the lunule, with the sides almost straight, sloping abruptly to an acute tip behind, and with the umbonal end bluntly, broadly rounded. Seen in profile, the post-dorsal slope of the right valve is always more concave than that of the left, which is nearly straight. The escutcheonal margin of the right valve is an acute fold, coincident with the *right* post dorsal slope of the shell, and the margin on the *left valve* is slightly medial to the post-dorsal slope, which in the *left valve* is a rounded angle. The margin of the *right* valve fits into a marginal groove of the left, again simulating a lateral tooth and socket.

Sculpture is very variable, although the two valves agree closely in whatever pattern is shown. At one extreme, the valves may have low, flat, poorly defined concentric ridges, spaced evenly over the whole valve, separated from each other by a groove of about the width of the ridge. These may be vague near the umbones and progressively more prominent toward the ventral margin. Other specimens (most of those in the Galveston area) may be completely without the ridges, or have them slightly manifest, or discontinuous, or they may be prominent near one dorsal margin only, or complete across

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FIG. 10. External view of the two valves of a shell of *C. martinicensis* from San Blas Islands, Panama (TABLE 1, No. 7). Height, 2.21 mm.

FIG. 11. Internal view of specimen in FIG. 10.

FIG. 12. *C. martinicensis* from San Blas, Panama (TABLE 1, No. 7). The specimen at lower right is 1.8 mm high. All loose valves; the right valves are in the two rows on the right side.

FIG. 13. *C. lunulata* from Heald Bank (TABLE 1, No. 1a). Shell is 7.15 mm high. See FIGS. 6 and 7.

FIG. 14. *C. martinicensis*, from Northwestern Gulf of Mexico (TABLE 1, No. 9). The three shells at top are complete; all others were loose valves; those in the three rows to the right are right valves. Shell at lower right is 1.2 mm high.

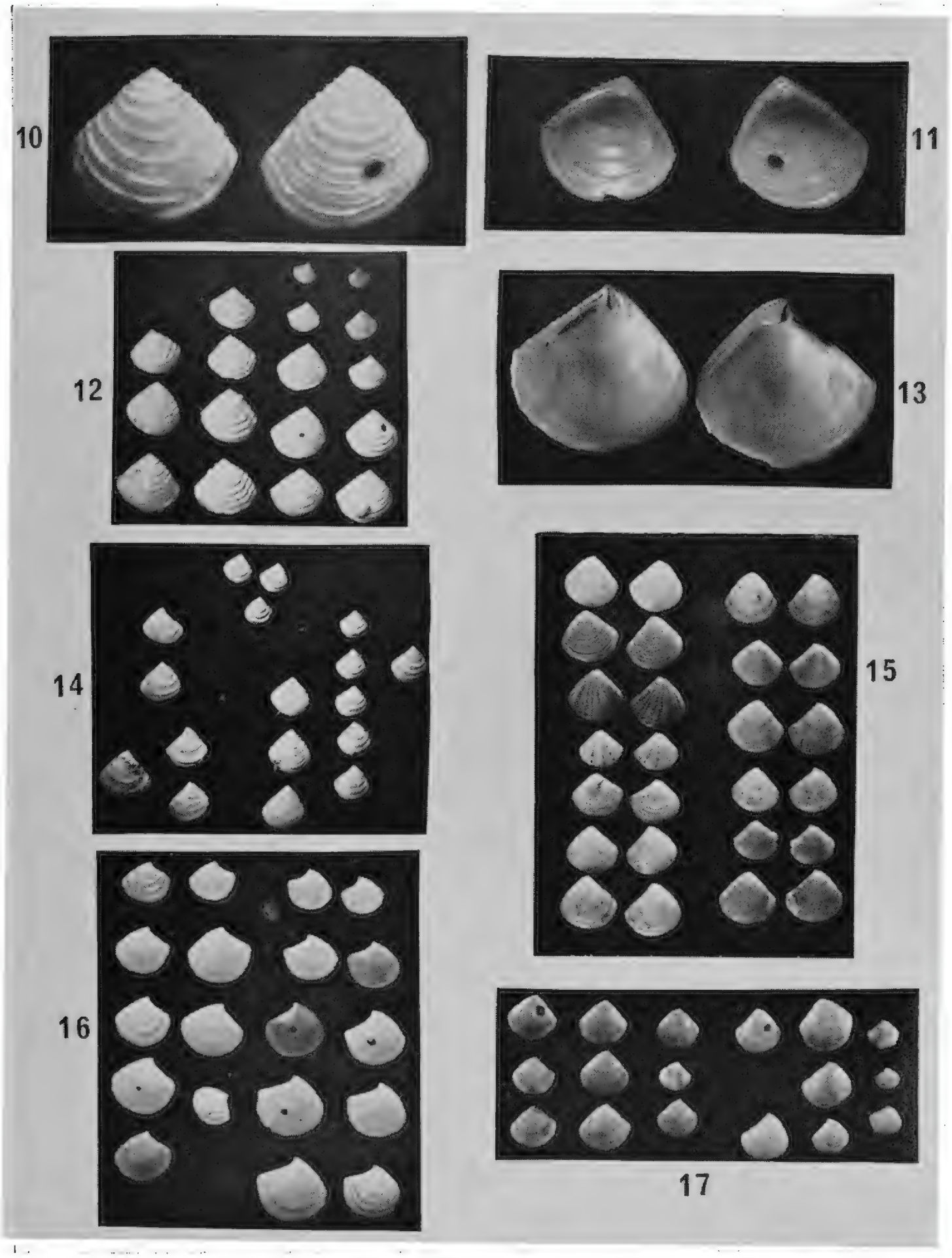
FIG. 15. *C. lunulata* from Heald Bank, near Galveston (TABLE 1, No. 1a). Pairs of valves of specimens used for anatomical study. Specimen at lower right is 7.28 mm high.

FIG. 16. *C. lunulata* from Heald Bank, (TABLE 1, No. 1a). Loose valves of juvenile shells. Right valves are in the two rows to the right, and the specimen in lower right corner is 2.21 mm high.

FIG. 17. *C. lunulata* from Galveston Bay (TABLE 1, station 2a). All loose valves when found; the 3 rows to the right are right valves, and the specimen at lower right is 3.51 mm high.

only part of the valve; every degree of variation between well ridged and smooth shells can be found in one lot. When the ridges are most perfect, there may be 19 to 23 per valve. Occasionally, as in the lot from off False Cape, Florida, the ridges may be replaced by thin, fragile and recurved lamellæ, like those generally present in *C. martinicensis* (see below).

The texture seems to be entirely a phenomenon of the external cuticle. It consists of



elongate, swollen, polygonal units, arranged in radiating rows, with the long axis of each polygon directed transversely (Fig. 9). The texture is uniform in all fresh shells. This outer sheet of cuticle is very tough, and easily obtained entire by digesting the shells in weak acid (5% HCl in 70% isopropyl alcohol). By this method it is possible to demonstrate that there are two layers of calcareous shell, an inner and outer, and between them a second layer of cuticle. The latter is thick, smooth, polished and brittle.

The interior of the valves is non-nacreous, with a waxy appearance. It is shallow, except for a small recess of variable depth under the cardinal hinge plate. The antero- and post-dorsal margins meet the disc of the valve in a rather sharp angle, owing to the peculiar use of the shell margins proper as lateral teeth. The ventral margin never has denticulations, but there is often a shallow, poorly defined groove along it. This is variable in its presence and prominence, often completely absent. Since it seems to be between the two shell layers, it is possibly a phenomenon associated with their differential growth, and may be present or absent in the same individual at different times of its life.

The abductor muscle scars may be flush with the surface of the shell, or in other specimens sightly sunk below it. The anterior one is bean-shaped (reniform), being concave behind and more acutely rounded at its top end, which is just under the valve margin. The posterior scar is sub-quadrate, a little elongate dorso-ventrally, with rounded corners and flattened sides. The anterior pedal retractor muscle scar is a small circle, above and well separated from the adductor scar. It is on the same plane (*i.e.* on the disc proper) as the adjacent adductor scar. The posterior pedal retractor scar is small, triangular, and confluent with the adjacent adductor scar, but situated under the edge of the shell, so that its plane of attachment is about at right angles to the plane of the posterior abductor. The pallial line is prominent, broad, and without a sinus.

Hinge: In the left valve, there is a deep, narrow groove along the post-dorsal shell margin which receives the post-dorsal margin of the right valve. On the inner bounding wall of this groove, at the lower third of its length, is a low, vaguely defined, elongate bulge projecting beyond the rest of this lamella, and fitting into a poorly defined depression under the right post-dorsal margin. There is a similar groove along the anterior dorsal margin of the right valve, to receive the left antero-dorsal shell margin. It also has a bulge on the lower third of the inner lamella, fitting into a vague pocket of the opposite valve. These two obsolete bulges probably represent the true lateral teeth of other species of heterodont bivalves. Their function in this species has been replaced by the inturned margins of the shell.

The umbonal area of the hinge is a triangular plate with free margin over the subumbonal cavity. There are in the right valve two cardinal teeth, with a narrow, deep tooth-socket between. The anterior right cardinal tooth is low, poorly defined, and almost parallel to the inner lamella of the lateral hinge margin socket. It does not extend to the free margin of the hinge plate. The free (medial) margin of this vague tooth is a sharp edge. The posterior right cardinal tooth is much larger, extending to the free hinge margin, with a flattened medial surface. In front of this tooth is a triangular depression containing the resilium and reaching from the umbo to the free margin.

The resilium resembles two elongate, slightly spiraled antelope horns, with their tips under the umbones and their bases at the margin of the hinge plate. These two parts touch only at their bases.

In the left valve there is an anterior cardinal tooth which is elongate, triangular, with its base along the hinge margin. This fits between the two cardinals of the right valve. Its anterior and posterior surfaces are transversely ridged, as are the opposing surfaces of the teeth of the opposite valve. These surface crenulations vary from prominent to absent in different valves, and may be correlated with growth periods. The anterior cardinal of the right valve fits between the anterior one of the left valve and the resilium.

The left valve has a posterior cardinal behind the resilium, along the upper half of the latter, which bends over it and fits between the resilium and post dorsal margin under the umbo of the right valve, where there is no well defined socket.

Color: Great variation in color of these shells results from combinations of only two factors: (1) The inner calcareous layer of the shell may have a vaguely defined wash of color, varying in shape and ranging from light tan to deep chestnut brown or even purple. When color is present in this shell layer the inner of the two layers of cuticle is also dark horn color and opaque, but this cuticular layer is colorless and transparent otherwise. (2) The outer, sculptured cuticular layer may be uniformly light to dark brown, or the color may be present only in rays which vary in width, number, intensity of color and continuity, sometimes being broken up into quadrate spots. There seems to be no pigment in the outer shell layer *per se*, but only in the outer cuticular sheet. The outer shell layer is white and translucent. In some specimens no brown color is present, and the shells are entirely white. In others, the outer cuticle may be colorless and the inner shell layer colored, or vice versa, and both the inner layer of shell and outer cuticle may be colored in still others. The species rivals *Donax variabilis* in the variety of color patterns.

The protoconch (needlessly termed prodissoconch in bivalves by some authors) is persistent, smooth, polished, subspherical, and about 0.14 mm long. The measurements of a typical large shell are: height 7.15 mm, length 9.00 mm, width 3.9 mm.

### *Gross anatomy of the soft parts*

The mantle inside the pallial line is very thin and transparent. The part between the pallial line and the margin proper is thicker, owing to more connective tissue and numerous margin retractor muscles, all of which originate exactly along the pallial scar of the shell. There is also a peculiar glandular organ shaped like a scythe blade, on the anterior part of the mantle margin. Its widest part is at the anterior end, just below the adductor muscle; it nearly occupies the whole of the area between the pallial line and mantle margin in its front half, but back of the middle of the shell it tapers slowly to an acute tip, well in front of the incurrent siphonal area. I could find no opening. The gland projects into the mantle cavity as a thick pad, and appears to be divided into dorsal and ventral parts, the upper being more translucent and larger, the lower more opaque. Both parts are white. When ruptured this gland exudes many minute colorless spheres about 0.1 mm in diameter, containing numerous oily droplets of varying size, the larger being 0.035 mm in diameter. In sections, this gland seems to have thin walls surrounding a large cavity containing the granules, which stain strongly with eosin. Such a mantle margin gland is present also in *Crassatella speciosa* A. Ad., where it has the same shape and position. It may thus be characteristic of the whole family, and is here named the

crassatellid mantle margin gland. This seems not to have been previously reported, nor have I observed it in any other family of bivalves.

The mantle margin has a deep, prominent outer marginal (cuticular or periostracal) groove. This always holds firmly a broad, inturned extension of the periostracum, which here shows very plainly the peculiar texture described for the external surface of the shell.

The inner of the 3 mantle margin lamellæ seems to be prominent only along the posterior half of the ventral margins. It is minute and thin. The two inner lamellae of the opposite mantle lobes are fused below the excurrent siphon, but not below the incurrent one. The mantle margin is thus completely open ventrally from the fusion between the siphons to the anterior adductor muscle. No part of it is papillate, even around the siphons. The mantle lobes seem to be attached to the subumbonal cavity of the shell but no scars could be found there.

Dorsal to the visceral mass the mantle projects as a thin lamella of considerable width between the hinge area of the shell valves. This fold extends between each inturned dorsal margin of the shell and the socket which receives them. Under the umbones this broad lamella is interrupted (Fig. 4). There is a large hole through which the bases of the bifurcate resilium make contact. Evidently the resilium grows by additions to its basal area, produced by the edge of the mantle forming the hole. In front of the resilium the dorsal mantle flange is broken up into three finger-like projections which seem to correspond to the cardinal teeth and sockets. Both abductor muscles are conspicuously divided dorso-ventrally into translucent (outer) and opaque (inner) parts, homologous to the quick and catch muscles of the Ostreidae and other "pseudolamellibranchs" (Figs. 1 and 3). In sections the inner or "quick" parts of these muscles are prominently striated, like the voluntary muscle cells of vertebrates, and the outer or "catch" parts are smooth muscle cells.

The gills are represented by only one demibranch on each side (Fig. 1). They are large, not pleated, and a prominent groove is present along the free (ventral) margin. The axis of the demibranch is straight, and parallel to the post-dorsal shell margin. Thus it is oblique in relation to the antero-posterior axis of the animal. This axis is attached along its entire length to the mantle, where the latter joins the epithelium of the visceral mass. Fusion of the gill axes to the mantle also continues behind the visceral mass. The gill filaments are suspended at right angles from the demibranch axis. The ascending rami of the filaments are turned medially, toward the body. The upper edges of the inner lamellæ are entirely free from each other and from the visceral mass. Along this margin the adjacent filaments are fused, and there is a prominent tubular blood sinus. The inner lamella is slightly narrower (in the dorso-ventral direction) than the outer. From this it appears that these demibranchs are homologous to the medial (inner) demibranchs of those bivalves which have two demibranchs present on each side of the body. The posterior ends of the gill axes are immediately anterior of the fusion of the inner mantle margin lamellæ between the two siphons. The two ascending lamellæ, although not attached to each other, are held close together in life, thus functionally but not structurally forming an efficient diaphragm.

At the posterior end of the gill the filaments are very short. They increase regularly and rapidly in length to a point below the umbones, which constitutes the widest part of

the gill. In front of that point the filament length again decreases, but more slowly, so that the most anterior filament is about as long as the gill axis. This filament is parallel to antero-dorsal margin of the shell. Its descending ramus is also attached throughout its length to the mantle, so that it superficially appears to be a continuation of the gill axis.

The 50 or so filaments in each demibranch are structurally connected in eulamellibranchian fashion by interfilamentar junctions, leaving large, elongate ostia, regularly arranged in rows parallel to the gill axis. Interlamellar junctions are present only in the lower half of the demibranch; whether they are mere rods or form sheets was not determined.

The labial palps are minute, of typical subtriangular shape in profile. Their posterior tips just overlap the anterior ventral margin of the demibranchs. The opposed lateral surfaces of the palps have a few minute dorso-ventral grooves.

Particles of fine carborundum move downward on the gill filaments and forward along the ventral groove. There are also bands of cilia which move particles forward along the top of both the descending and ascending lamellae. The lateral surfaces of the visceral mass are ciliated, moving particles backward, then ventrally along the posterior free margin of the visceral mass. On the mantle surface particles move ventrally, then posteriorly along the pallial line or a little below it; masses of particles incorporated in mucous (pseudofeces) pass out just below the intersiphonal junction of the inner mantle margin lamellæ. The pseudofeces must thus traverse the incurrent stream of water at right angles.

The front part of the foot is elongate and cylindrical. There is a small, rounded "heel" behind. The ventral margin is blade-like, but there is a deep, narrow groove along about half its length in the middle, which does not seem to extend to the anterior tip (Fig. 1). The byssal glands open into this narrow groove. Several alveoli, which can be seen as opaque, white, rounded objects near the hind end of the foot, project upward slightly into the visceral mass.

The internal organs have not been studied in detail. The liver occupies an elongate oval area under the antero-dorsal slope of the shell margin, and scarcely extends beyond the umbones. It completely surrounds the stomach, whose internal anatomy was not studied. A large, hyaline, crystaline style persists even after the clams have been starved for many days, but whether it was in a sac separate from the anterior end of the intestine was not determined.

After leaving the stomach, the intestine passes downward toward the foot. Then it forms a broad curve backward and upward toward the umbones, below which it again turns posteriorly, traversing the pericardium and passing through the ventricle of the heart. It then passes dorsal to the posterior adductor muscle, bends sharply downward and opens just in front of the excurrent siphon.

The pericardium and chambers of the heart are thin walled. There is no pigmented area of the pericardium or the auricles which might indicate a pericardial gland. The two auricles are triangular, with broad bases where the venous blood enters, with small openings that join the ventricle laterally.

The kidneys are two elongate, cone-shaped sacs, laid on their sides along the pericardium. Their concave bases conform to the contour of the posterior adductor muscle. These sacs join each other by a narrow passage midway of their length, but techniques

used did not permit finding a renopericardial passage or the renopore. There are no trabeculæ within the sacs. The peculiar granules of the kidney are described below (see pigments).

The gonads fill the greater part of the visceral mass, but do not extend lateral to the liver or along the rectum nor into the mantle. The sexes are separate. The ovaries are dawn-pink in color, owing to the color of the cytoplasmic granules in the eggs, to be discussed below (see section on pigments). The ovarian eggs from the October collections have an outer diameter of 200 microns, with a thin surface zone 15 microns thick which is hyaline and colorless (Fig. 2). A large, hyaline, seminal vesicle, 40 microns in diameter, is near the cell membrane. No nucleolus could be found in unstained preparations. The cytoplasm has numerous granules, three microns and less in diameter, clustered in a poorly defined zone at the surface of the cytoplasm.

The testes (Fig. 3) are whitish, branched organs, with large ducts, the ends of which are scarcely swollen. The testes seem to open separately from the kidneys, just below the latter. Presumably the ovaries open at the same place, but this was not demonstrated by the techniques used. The sperm have conical heads 9 microns long, and tails about 60 microns long. Most were very active in squash preparations, but many were quiet, forming a fuzzy, hemispherical mass with their heads attached to nurse cells projecting from the wall of the testes.

In a few female specimens from False Cape, Florida, collected in September, and also in the Heald Bank population of October, there were from four to twelve eggs in the interlamellar gill space, just below the kidney. These were each enclosed in a thin transparent membrane, and not attached to each other. Although none of these embryos was developed to the stage of having a shell (protoconch), I am inclined to think this indicates brooding occurs in this species, at least during early development. Another member of this family, *Cuna dalli* Vanatta, has recently been discovered to be ovoviviparous (Moore 1961), and evidence will be cited below indicating that *Crassatella speciosa* may also brood eggs, at least during early development.

Of the nervous system it was determined only that the visceral mass ganglia are large, oval bodies, touching in the midline, located on the ventral side of the posterior adductor muscle. The pedal ganglia are oval masses 1½ times longer than wide, slightly touching in the midline. They are located in the antero-ventral part of the visceral mass, just above the foot and behind the anterior pedal retractors. The cerebral ganglia are small oval bodies on each side of the mouth, connected to each other by a large commisure.

### *Pigments*

*Crassinella lunulata* has a much more colorful anatomy when examined in the living state than the more advanced heterodont bivalves with which most people are familiar. The liver, has the usual olive-green color in well-nourished specimens, which fades to light brown in fasting ones. There is a variable amount of brown and black melanin pigment along the post-ventral mantle margin. This may form a continuous strip, or only a few quadrate blotches.

If a live clam is opened out of water, the red color of the blood is easily seen, since the flesh is usually ruptured. Using a ten lambda quantitative capillary tube I could draw up less than one lambda of blood. This amount was enough to examine under a compound microscope and thus determine that the red color, which looks like hema-

globin in reflected light, also is straw colored in transmitted light. The color is dissolved in the plasma, and not contained in blood cells, in contrast to several species of Arcidæ.

Sprinkled over the inner surface of the dorsal part of the mantle margin gland, extending upward on the mantle above the palial line and often below the gland are numerous, minute, red dots. These have the same color as the blood, only the color is more intense. A chip of fresh tissue pressed out on a slide and examined at higher power showed these to be small vacuoles, perhaps one to a cell, with several similar cells clustered together, so that the color is grossly evident. The contents of these vacuoles appears to be a viscous fluid which is again straw colored in transmitted light. I have no further evidence (such as spectroscopic analysis), but this material may be hemaglobin, although contained in stationary cells.

There are larger bodies of this red fluid enclosed in what appears to be larger intracellular vacuoles in the cardinal part of the mantle margin which is inserted between the two valves along the hinge area (Fig. 4). Of these, one is in the anterior margin of the mantle hole surrounding the resilium, and there is one in each of the three digitiform processes associated with the cardinal teeth in front of the resilium.

Additional sites of hemaglobin in stationary tissue are the peripheral granules of the ova, which impart to the eggs and whole ovary a pinkish color. In a few bivalves of the Galveston area there is also tissue hemaglobin in the central nervous system (*Dosinia, Mulinia, Nuculana*), but this is absent in *Crassinella*, which has light yellow ganglia.

The foot is bright orange-yellow in fresh speciments. This fades in captivity, and may represent a carotene pigment which varies in intensity with the nutritional state. The location of this pigment within the cells could not be determined.

The granules of the kidney are small and light golden-amber in young specimens, but larger, dark grey-green in older ones. They are not dissolved by 5% hydrochloric acid. By their abundance the shape and extent of the kidney is prominently outlined. These may be retained secretion products, as Turchini (1923) has already suggested of similar granules in other bivalves.

## Behavior

*C. lunulata* is shy and lethargic, showing little movement in captivity. Rarely the single, excurrent siphon was seen extended beyond the shell (Fig. 5). This is transparent, colorless and short, rounded at the end and with a small hole. No part of the siphon is papillate. The foot is occasionally protruded, as a long digitiform, orange-yellow projection from the anterio-ventral part of the shell.

Left undisturbed overnight, *C. lunulata* often climbs up on bits of shell, or the sides of the aquarium. There they become attached and suspended by a very delicate byssal thread, which breaks at the slightest touch. In limited experiments, they made no effort to burrow into fine shell substrate, but the presence of a small patch of red calcium (algal?) deposit on several shells near the siphon suggests these do occasionally burrow, leaving just the posterior tip exposed. As climbers and byssal-attachers, they are much less active than the small *Arca transversa* which occurs with them in the Galveston area.

About half of the live specimens from off False Cape, Florida, had one or two live foraminifera attached to the posterior ventral part of the shell, and one specimen had a balanoid barnacle nearly as large as the bivalve itself attached to it. This again suggests these clams spend much of their time on top of the substrate, rather than buried in it.

## Ecology

Verrill (1873) cites *C. lunulata* (as *Gouldia mactracea*) in Vineyard Sound and Buzzard's Bay, Mass., as being quite common alive in gravelly, shelly, or sandy bottoms, while the dead shells were generally diffused. In a much more detailed paper of the same region Summer *et al.* (1913) list 179 stations of these two adjacent bodies of water in which this species was found (cited as *Crassinella mactracea*), with estimates of the number of specimens taken at each. For most stations the quantity cited is "one shell," or "few shells, one living." Only 15 stations yielded many shells or living specimens, indicating that while shells may occur diffusely over a larger area, it is found alive at only a few limited localities therein. They stress the point that it was found "for the most part on bottoms free from mud." It was found at most stations in Vineyard Sound, into which little freshwater enters, and which has a bottom chiefly of coarser substrate material (glacial gravel, boulders, shell and sand). In Buzzard's Bay, it occurred chiefly along the shore of Woods Hole Cape and the Elizabeth Islands, which separate the sound from the bay. Buzzard's Bay has a somewhat greater influx of fresh water and a bottom mostly of mud. They cite *C. lunulata* as occurring from 3 to 17 fathoms (24 fathoms is about the maximum depth of the area, and poorly explored).

Summer *et al.* (1913) noted that the surface temperatures of the area varied seasonally from 3.9 C (39 F) in February to 20.56 C (69 F) in August, and bottom temperatures seemed to vary usually less than 1 C from that of the surface. The maximum range of salinity reported for the stations wherein this species occurred was 30.9 to 32.9 ppt.

No reports of the ecology of this species have been found for the Atlantic coast south of Massachusetts. The meager data of its occurrence in Florida suggest it may enter more shallow depths than it does in New England and in the northwestern Gulf of Mexico. Dall (1883b) cited it (as *Crassatella (Eriphyla) lunulata*) as abundant on the beach of Sarasota Island; Perry (1940) cited it occurring in southwestern Florida in "less than one to six fathoms." Beginning with d'Orbigny (1846), several faunal accounts of the Antilles cited this species and *C. martinicensis* occurring as beach shells, but it is very doubtful that these species live intertidally. Abbott (1958) cited it (as *Crassinella guadalupensis*) as dredged alive from nine stations within North Sound of Grand Cayman Island, where the bottom was muddy and the water six feet deep.

In the northern Gulf of Mexico records of *C. lunulata* under various names are numerous, often with bits of significant ecological data. Vanatta (1903) cited *C. lunulata* from three localities near Apalachicola, Florida, in the northwestern part of the state (probably reporting beach shells). Moore (1961) noted that occasional shells of *Crassinella lunulata* wash ashore on the Gulf side of the barrier islands of Mississippi. He found it alive (only 2 specimens) in Dog Keys Pass at the west end of Horn Island. This pass has a depth of 20 to 50 feet (Moore 1961:6). For this station, which was the most seaward of the several included in his study, he reported a bottom salinity ranging from 27.75 to 33.93 ppt, one of the highest and most constant for the coast of Mississippi. The bottom temperature at that station ranged from 19 C (Dec. 1956 )to 29.7 C (June 1957), and lower temperatures are thought to occur there. Although Moore notes this species as a "sand dweller" (1961:40) he elsewhere (*l.c.*, p. 11) indicates that the substrate of Dog Keys Pass has a high component of broken shell.

Parker (1956) cited *Crassinella lunulata* from 31 stations, but alive at only two, in

upper Breton Sound, north of the Mississippi River delta in Louisiana. He misidentified this as *C. martinicensis*, as Abbott (1958) has already noted. The figures (Parker 1956, pl. 2, Figs. 12a, 12b) obviously represent a partly smooth shell of *C. lunulata*, as does the reported size, 8 × 7 mm. The area of Breton Sound in which *Crassinella* is reported is 2 fathoms deep or less, but characterized by relatively high and constant salinity which "seldom falls below 28 ppt even during the flood stages of the Mississippi River" (Parker, *l.c.*, p. 326; reported as a chlorinity of 16 ppt).

Parker (1955) also cited *C. martinicensis* living in Aransas Bay, Texas; this is probably again a misidentification of *C. lunulata*, for he cited it elsewhere from there under the latter name with confirming figure (Parker 1959, Pl. 3, figs. 9a, 9b), and noted it is characteristic of the inlets into Aransas Bay. Ladd (1951; 1957) cited "*Crassinella* sp." from several stations in Aransas Bay, Redfish Bay, and Aransas Pass, Texas, and 2 to 4 miles off shore from those localities. It was found in several other, more shoreward bays of the area. He noted that depths exceeding 9 feet occur only in Aransas Bay of those considered, and the station within Aransas Pass where it occurred was 18 feet deep with much shell in the substrate. The average salinity for the bottom of the bay was 21.7 ppt. The average salinity of the offshore station at the bottom was 36.1 ppt. Pulley (1952) cited dead shells of "*Crassinella mactracea*" at Galveston and Port Aransas, Texas, and "living shells in Galveston Bay."

Most of the living *C. lunulata* of the present study came from Heald Bank, a popular fishing area some 30 miles southeast of Galveston (Table 1, Nos. 1, 1a). This seeems to be an ancient sand bar, perhaps dating to the Pleistocene. The substrate has a large component of shell fragments. Although occasional fossil shells of *Crassostrea virginica* occur there, none have been found alive. Some 70 species of mollusca were taken there in one small dredge haul in June 1965, not to mention a number of other invertebrates, including abundant amphioxus (*Branchiostoma*). Water depth over this bar is only 5 fathoms. Depths of 7 or 8 fathoms prevail over most of the area between the Bank and the mainland. The bottom of that area is mostly fine grey mud with little shell. No *Crassinella* has yet been found there.

No hydrographic data are available for the precise locality from which *C. lunulata* was collected on Heald Bank. However, by extrapolating from the monthly values of nearby stations at which bottom temperature and salinities were taken by the U.S. Fish and Wildlife Service, Galveston, a reasonable approximation of conditions at Heald Bank may be obtained. On this basis, the bottom temperature may range from about 11 C in January, gradually warming to about 30 C in August. Similarly bottom salinities may range from about 33 to 36 ppt during the year. A variation this small at such a high level of salinity may not be critical for *Crassinella*, particularly in view of the wide fluctuation known to occur at the station where it lives within Galveston Bay.

A second colony was found alive in lower Galveston Bay at the intersection of the Houston ship channel and Intracoastal canal (Table 1, Nos. 2, 2a). This has an artificial depth of 42 feet, whereas most of this bay complex, outside of the dredged ship channels, is less than one fathom deep. The bottom at this station has a large component of shell, similar in appearance to that of Heald Bank. The ship channel station has mostly molluscs of the lower bay, plus *Donax variabilis* shells which seem to be all fossil. Besides *C. lunulata*, only a few species of molluscs are common to this station and Heald Bank, and rare elsewhere in the area (*e.g. Semele nuculoides* Conrad).

Hydrographic data on this station furnished by the U.S. Fish and Wildlife Service, Galveston, indicate that the bottom temperature may be 10 to 15 C during January and February, gradually and irregularly warming to 29 C during August and September. The bottom salinity possibly fluctuates more frequently than the bi-monthly sampling techniques indicate (perhaps even daily, due to tides). Differences of 6 or 10 ppt were not unusual during spring and early summer at two weeks intervals, whereas differences of less than 4 ppt were encountered from August through December. The salinity ranged from 26 to 33 ppt during the latter period, 18 to 30 ppt from February through April, and only 15 to 21 ppt during May and early June. These salinity values are nonetheless among the higher ones which can be expected in Galveston Bay.

*Crassinella* must certainly be rare as a beach shell and in most of the dredged bay samples at Galveston. I have found it at only one other station in Galveston Bay, at 3 m depth just east of the lower end of the Texas City dike (No. 3, Table 1). Perhaps this is a spoil bank, dredged from the near-by ship channel. This is suggested not only by similarity of shell fragments and biota, but also by the aspect of the shells of *C. lunulata*, none of which were alive there. The modal size of shells from the shallow station is very close to the modal size of those from the ship channel (*cf.* Sta. 2, 2a and 3 of Table 1).

The sample of *C. lunulata* taken off False Cape, Florida was also from a shelly bottom (Table 1, No. 4). The substrate of sample No. 6 of Table 1 was chiefly mud, however.

In summary, it may be noted that *C. lunulata* is known to occur from Cape Cod to Florida and the Antilles, and along the Northern shore of the Gulf of Mexico at least as far as Aransas Pass. It also occurs on the Campeche Bank bordering Yucatan. Generally it lives on a bottom of coarser particles and seems to occur in small colonies. It inhabits only depths below low tide throughout most of its range, but dead shells occasionally may be found on beaches, and further work may find it in shallower water in the warmer parts of its range. It is probably more limited in its range by low salinities than by low temperature (if indeed either are directly limiting factors). In the northwestern Gulf of Mexico it seems to occur sporadically off shore, but inside the bays it is found alive only in the deeper tidal passes which have usually been artificially dredged. Dall (1881) reported it (as *Crassatella (Eriphyia) parva*) as ranging downward to depths of 287 and 1,568 fathoms. However, in 1889 he recorded it from 3 to 100 fathoms and its "variety *parva*" from 15 to 287 fathoms. The lower bathymetric limits of this species are therefore doubtful.

The biotic relationships are even less well known. In nearly every sample there is evidence of drilled shells (Figs. 10, 11, 12, 16, 17) suggesting the work of some predaceous gastropod, and small Naticidae were found in most samples examined. Frequent broken shells suggest the work of crabs or fish. The single valve from which Linsley (1845) described "*Astarte mactracea*" was taken from the stomach of a haddock.

At most stations where *Crassinella* was found there was an abundant and varied fauna of mollusca and other invertebrates, suggesting that this genus prefers eutrophic conditions.

## Parasites

A bucephalid trematode was found in about 7 out of 10 of the larger specimens (height greater than 5.2 mm) of *C. lunulata* from the October sample of Heald Bank. None of the 4 specimens found alive in Galveston Bay in October was infested, nor were any of

the 10 specimens from Heald Bank examined which were below 4.7 mm height, nor any of the 9 specimens with animal from False Cape, Florida. No precise studies of the larval stages were made. The number of species, from fish, of this group known as adults would preclude a hasty identification. However, this species closely resembles *Cercaria apalachiensis* (Holliman 1961) from *Mulinia lateralis* of Apalachee Bay, Florida.

None of the cercariae from Heald Bank were found emerging, or even free in the hemocoel of the clam. When liberated from the sporocyst these cercariae remained stationary, but stretched and contracted their bodies and tails. The tails frequently broke off and continued to contract. The sporocysts were light-yellow, due to greenish-yellow particles (which may be liquid) in the sporocyst. The particles measure 4.5 microns and less in size. In the connective tissue around the sporocysts are masses of bright orange granules, each mass being about 7.5 microns long. These were not found in non-infected clams.

No evidence could be found of the gonad in infested specimens. The position of that organ is almost exactly that occupied by the mass of sporocysts. Probably these clams are somehow castrated by the worms, even though the sporocysts may feed only by absorption of substances dissolved in the clam's blood. The sporocysts do extend upward, lateral to the liver. However, as evaluated by gross observation their damage to that organ seems to be minimal and secondary, as in most molluscs parasitised by trematodes, contrary to orthodox views of parasitologists. Whether the larger size of the Heald Bank specimens is due in part to hypertrophy associated with parasitic castration must await more evidence for an answer.

## Variation in Size

Variation in shell color, sculpture, and shape in populations which I consider to be *C. lunulata* have been dealt with above. Another variable which has been suggested to be of value in differentiating species of *Crassinella* is size. Simple inspection shows that specimens from one station considered collectively are mostly larger or smaller than those from another. This variation is most conveniently expressed mathematically by comparing the terminal modal size of each population. As an arbitrarily chosen parameter of size, height was measured for each loose valve and conjoined pair to the nearest 0.13 mm, using an ocular micrometer in a stereoscopic microscope. The data were then grouped in classes of 0.507 mm range, and the class frequencies determined.

In larger samples there were two or even three modes. Always there was one mode near the maximum size. This terminal modal class may represent the characteristic size of the adult population. An exact expression of this modal size was then determined by the formula:

$$\text{Mode} = L + \frac{f_2}{f_1 + f_2} w$$

where L is lower limit of the modal class in mm; W is the difference between the limits of each class in mm; $f_1$ is the number of individuals in the class below the modal one, and $f_2$ is the number of individuals in the class above the modal.

From Table 1 it is evident that the terminal mode of populations from different localities varies greatly, but the mode of the same population re-collected after a period of months remains relatively constant (*i.e.*, stations 1, 1a and 2, 2a). The terminal mode is always larger than the median, which may be obtained by dividing the maximum size by

two, since the minimal theoretical size (*i.e.*, the height of the protoconch) is only about 0.14 mm, and this may be counted as zero for present purposes. In nearly every case the terminal modal height is also larger than the average height (also listed in Table 1) of a population. Moreover, the average size of the same population seems to vary more than the terminal modal size (Sta. 1, 1a, and 2, 2a), as might be expected since the presence of juveniles might influence the data more at one season than at another.

Number 6 of the table probably does not show the true terminal modal size of the population from its station. Although the shells of that station are very typical of *C. lunulata* in sculpture and degree of inflation, the sample is very small.

## Taxonomy of the Species

Verrill (1873) early recognized that there was only one species of *Crassinella* along the east coast of North America and that this was present also in the northern Gulf of Mexico. He called it *Gouldia mactracea*, but implied that the species might be identical with Conrad's Miocene fossil, *Astarte lunulata*, of which he had no material. Dall (1903) thought these two species differed only by the radial texture of the former, and since this is chiefly if not entirely a phenomenon of the cuticle, it would scarcely be present in fossils.

Abbott (1954) recognized *C. mactracea* as extending from Massachusetts Bay to Long Island, and *C. lunulata* from "North Carolina to both sides of Florida and the West Indies," but it is scarcely possible to differentiate two species from his descriptions, and moreover the figure he published of *C. lunulata* (*l.c.* p. 83, Fig. 28 K) is obviously the one Verrill (1873, pl. 29 Fig. 207) originally drew to illustrate *C. mactracea* of New England.

While the smooth shells on which Harris (1893, 1895) based the name *galvestonensis* may be more common in the northwestern Gulf of Mexico than along the east coast, all degrees of shell sculpturing occur in both the Heald Bank and Galveston Bay populations (Figs. 15, 16, 17). Maury (1920) recognized *C. lunulata* and *C. galvestonensis* as distinct species, probably on the basis of whether the shells were smooth or costate. She noted that both are living along West Florida and at Galveston, and both are fossil in the Miocene of Maryland, New Jersey and Virginia. Evidently the smooth variant is widely distributed in time and geographically, and the name *C. galvestonensis* is thus not worth recognizing as a valid biological species or subspecies.

E. A. Smith (1881) early recognized that the *Thetis parva* C. B. Adams and *Crassatella guadalupensis* d'Orbigny were both identical with *Astarte mactracea* Linsley. The figure of the paratype of *T. parva* provided by Clench and Turner (1950) supports his conclusion, as do the original figure and description of *Crassatella guadalupensis* d'Orbigny (1846). These two nominal species fall within the range of variation of populations of *C. lunulata*, although several recent papers on the mollusca of the Antilles persist in recognizing *C. guadalupensis* as a distinct species (Dall and Simpson 1901; McLean 1951; Abbott 1958; Warmke and Abbott 1961).

The *Crassatella (Eriphyla) maldonadoensis* Pilsbry (1897) described without illustration from Maldonado Bay, Uruguay, is very similar if not identical with *Crassinella lunulata*, with which Pilsbry originally compared it. The size, (4.75 mm long, 4 mm high, 1.9 mm wide) and color ("pink" external rays, and "pink" inside the valves)

argue against its being associated with *C. martinicensis*, although Lamy (1917) placed it with the latter species. I have seen no specimens from South America.

*Crassinella martinicensis* (d'Orbigny 1846)
(Figs. 8, 10, 11, 12, 14)

*Crassatella martinicensis* d'Orbigny 1846, in Sagra, Hist. . . Cuba, Mollusques, 2:288–289, Pl. 27, figs. 21–23. Type locality, Martinique.

Shell similar to *C. lunulata*, differing chiefly in these characters: the umbonal angle is usually only 90° or slightly less, and the two dorsal slopes are usually of equal length and straight, with a greater width of the shell than in *C. lunulata*, *i.e.*, the valves are proportionately more convex. The concentric ridges are always present and continuous over all parts of the valve. They are always thin, and stand up prominently, being in the fresh state curved ventrally to form a half cylinder; the free margin is frequently broken, leaving an acute, ventrally sloping lamella. Nine to 12 of these may be present on a shell of maximum size.

Most shells are relatively thin and white, and no color is ever present in the interior layer. Rarely the external cuticle shows a faint wash of light brown toward the posterior part, and even more rarely two or three faint, discontinuous, radial pin-stripes of light brown. The textural pattern of the cuticle appears to be more prominent than in *C. lunulata*.

The terminal modal size and other data on measurements of the three populations of this species studied are given in Table 1. *C. martinicensis* seems never to surpass a height of 2.73 mm. Dimensions of a typical shell are: height, 1.43 mm; length, 1.43 mm; width, 0.78 mm.

A series of 20 fresh valves of juvenile *C. lunulata* from Heald Bank which were within the size range of *C. martinicensis* could be easily separated from even the more compressed specimens of the latter species, on the basis of the concentric lamellae (Fig. 16). The young *C. lunulata* closely resemble the adult in usually having the concentric lamellae flattened, rounded, and varying in prominence and continuity. Admittedly some very young specimens of *C. lunulata* from other stations (False Cape, Florida) have sharp lamellae and little color in the shells. Moreover, the shape and convexity of *C. martinicensis* shells sometimes approaches these characters in *C. lunulata*, but the color, size, and usually the sculpturing are then typical of *C. martinicensis*.

The case for distinguishing *C. martinicensis* from the group of nominal species synonymized above with *C. lunulata* has gotten almost universal support. Only Dall (1886; 1903) thought the two were identical, but the descriptions of these two species by Dall and Simpson (1901) express very well their differential characters (although they call *C. lunulata* by the name *C. guadaloupensis*). Nevertheless, the question of speciation in this group must remain unsettled. Whereas it is relatively easy to distinguish two species when populations are considered ensemble, admittedly some isolated specimens could with justification be referred to one species as easily as to the other. Lamy (1917) compromised the issue by recognizing *C. martinicensis* as a subspecies of *C. lunulata*. It is significant that whereas the larger species seems to extend into the tropics, at least along the Antilles and Yucatan, the smaller species seems limited to that area, and does not extend as far into temperate waters as does *C. lunulata*.

*C. martinicensis* has been previously known only from the shores of the Caribbean Sea (discounting Parker's misidentification of *C. lunulata* in the Gulf of Mexico under this name). I have found only one paper which presents any very exact ecological data on this species, and that may not be based on living specimens. The "*Crassinella guadalupensis*" which Garcia-Culeas (1963) cites in his ecological study of Laguna de Terminos, an enclosed bay of the Gulf of Campeche, is probably *C. martinicensis*, judging from the figure (*l. c.* pl. 1, fig. 6) of one of the two specimens found during his study. This was found at a depth of less than one fathom; the temperature ranged from 26 to 31 C, and a salinity of only 16 ppt is cited. As the shallow station from which it came is from the mouth of a river, it is likely that the salinity shows much variation during one year.

In the present study, material was available from two stations off the Caribbean coast of Panama (Nos. 8 and 9 of Table 1) and from a station in the northwest Gulf of Mexico about 100 miles southwest of Marsh Island, Louisiana (No. 7 of Table 1).

The panamanian population of No. 8 in Table 1 lived in a substrate of coarse particles (about 1 cm diameter or less), of greenish grains resembling glauconite, and cup-shaped bryozoan colonies. The other two populations lived in a substrate of mud, with very little shell material. The depth range is from 15 to 25 fathoms. No data are available on salinity or temperature, but at least the latter is probably high and constant, as the salinity may be also. Although no material was available for anatomical studies, the numerous fresh valves indicate it is probably living at those stations.

## Comparison with other Species

I have been able to examine a single preserved specimen of *Crassatella speciosa* A. Adams (1852) and dead shells from four stations, all of 25 fathoms depth in the Northwestern Gulf of Mexico, kindly provided by the U.S. Fish and Wildlife Service, Galveston. This is usually cited in the literature as *Crassatella floridana* Dall (1886) and *C. gibbesi* Tuomey and Holmes (1856), names which, as Lamy (1917) noted, must give way to their senior synonym used here.

*Crassatella speciosa* and *Crassinella lunulata* agree anatomically in several significant features. The greatest width of the gills is below the umbones, with the filaments rapidly decreasing in length before and after that point, giving the gills a peculiar shape. The anterior filaments of each gill are relatively long and attached throughout their length to the visceral mass. The medial demibranchs are not attached to each other behind the visceral mass (*i.e.*, no true diaphragm is formed). Both species seem to brood the early embryos, at least. The gills of neither species are pleated. However, Ridewood (1903) declares the gills of *Crassatella floridana* (*i.e.*, *C. speciosa*) to be pleated. Possibly he misidentified his material, for he found non-pleated gills in two other species of *Crassatella*. *Crassatella speciosa* agrees with *C. lunulata* in having minute labial palps, and open mantle lobes, attached to each other only below the excurrent siphon; in having the posterior pedal retractor's origin adjacent to the posterior adductor muscle and its scar confluent with the latter, but on a different plane, at right angles to it; in having a similarly shaped foot with a byssal groove along the ventral margin; and in the presence of the crassatellid marginal mantle gland.

The species differ in these respects: four complete demibranchs are present in *C.*

*speciosa*, but the outer ones are not attached to the mantle behind the visceral mass. The lateral teeth of *C. speciosa* are large, true laterals, not merely inturned shell margins. There is no obsolete denticle on the inner lamellae of the sockets receiving these laterals, such as occurs in *Crassinella*. The umbones of *Crassatella speciosa* are orthogyrous or slightly prosogyrous (contrary to Chavan 1939:33) while the umbones in *Crassinella* are strongly opistogyrous. The kidney of *C. speciosa* is a single cuboidal sac with internal trabeculae, situated on the same level with the pericardium and entirely behind it. It is traversed by the post pedal retractor muscles. The kidney of *Crassinella* consists of two prone cones ventral to the pericardium, apparently not trabeculate within, and not inclosing the pedal retractors. The incurrent siphon of *C. speciosa* has small papillae along the inner mantle margin lamellae, where there are no papillae in *Crassinella*. The periostracum of *Crassatella* is without polygonal sculpture. The radial color bands, absent in *C. speciosa* and most species of *Crassatella*, do occur in at least two, *Crassatella heteroglypta* Pilsbry of Japan, and *Crassatella paeteli* von Maltzan from the west coast of Africa.

These differences I evaluate as representing different genera, rather than families. Of course, all such evaluations are entirely arbitrary. Moreover, such a decision must await a comparison of the anatomies of the type species of these two genera, neither of which has been presently studied.

Species of *Crassinella* analogous to the western Atlantic ones are present on the Pacific side of tropical North America, as Lamy (1917) noted. *C. lunulata* is represented by *C. pacifica* C. B. Adams, (perhaps including *C. oregonensis* Keen 1938 as a northern representative), and *C. martinicensis* by *C. varians* Carpenter. A number of recent and fossil nominal species exist on the west coast, which may ultimately be recognized as synonyms of these. How distinct morphologically the west coast populations are from those of the Atlantic requires further study. Certainly the figures and descriptions available (*e.g.*, Keen, 1958) show no difference whereby the west coast species can be separated from the Atlantic ones.

Although *Crassinella* is usually thought to be limited to the American coasts there are a number of small crassatellid species from other parts of the world which may ultimately be referred to this genus (*e.g.*, *Crassatella torresi* E. A. Smith 1885 from New Guinea). The genus is known to extend at least to the Eocene of North America, (Palmer and Braun, 1965). Chavan (1939) suggests that a species of "*Gouldia*" figured from the Cretaceous of New Jersey may also represent this genus.

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# Biology of the Red Snapper, *Lutjanus Aya* Bloch, of the Northwestern Gulf of Mexico[1]

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## Abstract

Adult and juvenile red snappers were collected at irregular intervals in the northwestern Gulf of Mexico from February 1964 through March 1965. Stomach analyses indicated that red snappers were polyphagous. Adult red snappers were primarily piscivorous, although in certain seasons, they fed heavily on tunicates. Juvenile red snappers fed primarily on crustaceans, but periodically took fish. Age-growth studies conducted via scale readings indicated that red snappers have a more rapid growth rate than other lutjanids. It was found that *Lutjanus aya* attained a standard length of 200–220 mm their first year, and grew 80 to 90 mm each successive year up to spawning class III. The spawning season for red snappers off the Texas coast was found to be June to Mid-September, with the peak occurring in August. Adult red snappers seemed to prefer areas of hard limestone bottoms or irregular bottom formations, although commercial catch data and food studies indicated that they were not confined to these areas. Juveniles were collected only in waters over sandy and muddy bottoms, indicating that they do not show a complete preference for limestone bottom or irregular bottom formations.

## Introduction

The red snapper, *Lutjanus aya*, has long been regarded as an important sport and commercial fish of the Gulf of Mexico. Fishing of this species began on a commercial basis in Pensacola, Florida in 1870 (Jarvis, 1935). Since that time it has grown to be the third largest fin fishery in total pounds caught, and second in value, on the Gulf Coast (Anonymous, 1964). In addition to its commercial value, the red snapper has become one of the most sought after sport fishes on the Gulf Coast, attracting both party boats and large outboards to the offshore oil rigs and snapper banks (Kalman, 1965).

Voluminous literature concerning red snappers exists, but only a few papers contain information concerning their biology. Most of the early literature deals with exploratory cruises in search of snapper fishing grounds (Smith, 1885a, 1885b; Collins, 1887; and Adams and Kendall, 1891). Attempts to improve fishing methods and gear were made by Stearns (1885), Jarvis (1935), Smith (1948a, 1948b), Springer (1951, 1953), and others. More comprehensive works concerning the red snapper fishery were reported by Stearns (1885), Jarvis (1935), and Camber (1955). Most of the available information concerning the biology of the red snapper was summarized by Camber (1955) but many of his results were inconclusive.

The present study had two objectives. One was to ascertain the general biology and ecology of red snappers. The other was to compare the food habits of adult and juvenile snappers from Louisiana and Texas waters.

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## Materials and Methods

Both adult and juvenile red snappers were collected at irregular intervals in the northwestern Gulf of Mexico from the Mississippi River to Brownsville, Texas, during February 1964 through March 1965 (Fig. 1). During this period of time, various vessels and types of equipment were utilized in the collection of fish and the recording of physical and chemical data. Collections of snappers were made from the U.S. Bureau of Commercial Fisheries' *R/V Oregon* (*Oregon* Cruise 90) of Pascagoula, Mississippi, U.S. Bureau of Commercial Fisheries' *M/V Gus III* (*Gus* Cruises 19, 21, and 22) of Galveston, Texas, and on the *M/V Lorene* and *M/V Vagabond* of the Institute of Marine Science, Port Aransas, Texas. Most juveniles (young of the year, spawning-class 0) were collected with shrimp trawls, and adults were collected with handlines. No trawling was done on the "snapper reefs."

In addition to the above collections, length frequencies, body depths and scale samples were taken from large snappers brought into fish houses at Port Aransas and Aransas Pass, Texas. These fish were taken in February and March 1965 between Port Aransas and Port Isabel, Texas.

Standard lengths were determined to the nearest mm of all snappers collected.

Stomach contents were analyzed and the volume of each different food item was measured by displacement of water in a graduated cylinder. Excess fluid was blotted from the food material, before the volumetric measurements were made.

Impressions of three to four unregenerated scales were made on acetate slides 0.02–0.03 inches thick with a Connecticut Fish Scale Press. In order to make satisfactory impressions of scales from larger fish, the acetate slides were dipped in a 50% water,

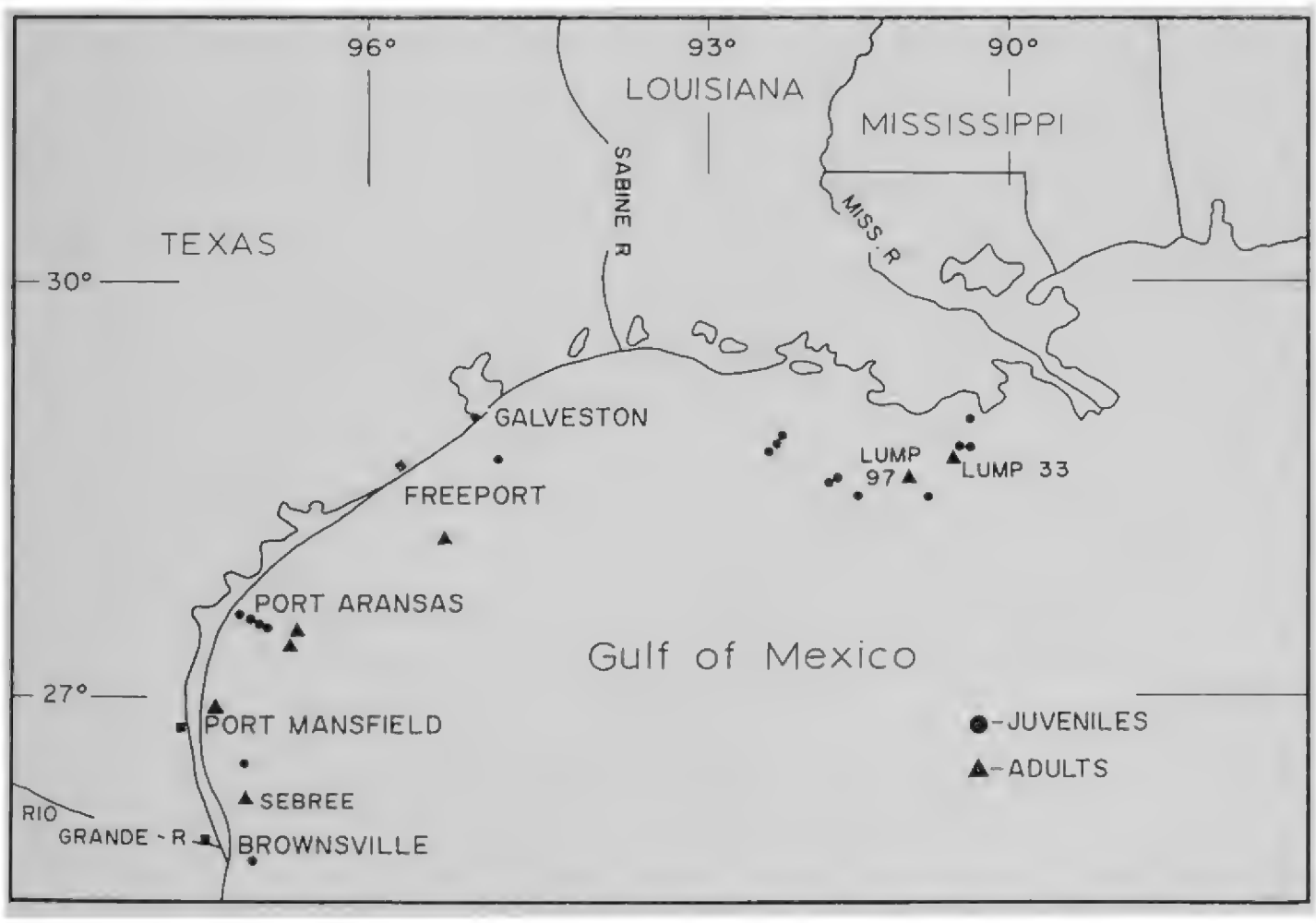


Fig. 1. Collection Stations for Red Snappers, Feb. 1964–March 1965.

50% acetone solution for about 10 seconds. The slides were blotted dry and scales immediately pressed. Scale impressions were viewed through a binocular dissecting microscope.

## Results and Discussion

### Distribution and Habitat

*Lutjanus aya* has been reported from Brazil to Massachusetts, with the largest concentrations being found off the Yucatan Peninsula and the Texas and Louisiana coasts (Camber, 1955). Camber also reported that snappers concentrated in relatively confined areas of hard limestone bottoms and irregular bottom formations. Most adult fish collected in the present study were taken from waters over these bottom types. In contrast, almost all juvenile snappers were collected from waters over sandy or muddy bottoms. Thus, juvenile snappers are not confined to irregular or hard bottoms. Commercial catch data indicated that adult snappers might not be as confined to irregular or hard bottoms as previously believed, and this is further supported by food data taken in the present study.

Red snappers are reputedly deep water fish, occasionally moving into shallow waters. Springer and Bullis (1956) reported depth records from 7 to 100 fathoms, mostly from the northern Gulf. Since no length frequencies were recorded, it is not known if the shallow water records were juveniles or not. Camber (1955) reported a few red snappers in commercial catches from 100–120 fathoms from Campeche; although, they tended to be more abundant in waters from 20 to 80 fathoms. Adult red snappers are more common in deep waters off the Texas Coast, but successful fishing has been reported in 7½ fathoms off Port Mansfield. Occasionally cold fronts cause red snappers to move into deeper waters for short periods of time during winter.

Occurrence of adult red snappers in shallow waters was also noted from sport fishing catches from the Aransas Pass Channel in October 1964. These fish were caught for only about a two-week period, after which it was assumed they moved into deeper waters.

Temperature ranges of the red snapper are virtually unknown. Springer and Bullis (1956) reported red snappers at temperatures ranging from 16 to 24 C on the bottom. Red snappers were taken in the present study from waters with a bottom temperature of 14 to 30 C. Fish taken at 30 C were small juveniles collected in September 1964 off Port Aransas. The record at low temperature was composed of adult snappers taken in February 1965 at 7½ fathoms off Port Mansfield. I was able to collect only a few specimens (190–337 mm), although fishing effort was comparable to other attempts. One week earlier, however, fishermen took a large number of snappers from this area. It is assumed that a cold front which occurred during the intervening period drove most of the snappers to deeper waters. Thus, it may be postulated that red snappers prefer waters warmer than 14 C.

As with temperature tolerances, little is known of salinity effects. In this study salinity ranged from 33 to 37 ppt, although data were not collected at critical times. Jones, Copeland and Hoese (1965) reported salinities only slightly lower than 33 ppt for the Port Aransas area.

## Migration

Except for some offshore migration during cold fronts, no data from the present study indicated any movement patterns. Topp (1963) and Beaumariage (1964) presented some data on tag returns of snappers off the Florida coast. Although long-term returns from release data were small, their data indicated little movement of adult snappers.

Adams and Kendall (1891) and Camber (1955) suggested that as red snappers grow, they seek deeper waters. For comparable trawls at 6, 9, 12, 15, 18 and 21 fathoms, I found juvenile snappers more abundant at 9 fathoms in September 1964 and at 18 fathoms in October. Since temperature and salinity were comparable, it was not clear why this offshore movement occurred, unless food availability was greater in the offshore area. No juveniles were taken off Port Aransas after October, although trawl samples were taken as deep as 18 fathoms.

## Spawning

Camber (1955) reported the spawning period of red snappers to be July to mid-September, with the peak occurring in July and August on the Campeche Banks. Baughman (1943) found a large ripe female red snapper during May, and a small juvenile (45 mm) during July off the Galveston coast. Thus, it may be concluded that the spawning season off the Texas coast extends from early June through mid-September.

The smallest juveniles found during the present study were taken off Port Aransas in September 1964 and averaged 49 mm in standard length. These fish were taken at the same stations sampled by Miller (1964). He sampled these stations in the late winter, spring and early summer and did not report red snappers in his collection. It is assumed that spawning usually does not occur in the Port Aransas area until late July or early August, but may occasionally be earlier.

Adult snappers caught during June off Freeport were quite varied in gonadal development. Fish taken in this sample ranged from 223 to 456 mm standard length. In general, the smaller fish showed less gonadal development than did larger fish, but exceptions were noted. Some fish ranging from 130 to 170 mm collected in February 1964 off Louisiana also varied in gonadal development. The gonad development of none of these fish was very advanced, but sexual differences could be noted. Similar variation was noted in fish ranging from 200 to 400 mm collected off the Texas coast during February 1965. It is therefore believed that some red snappers do not spawn their first year.

No specific spawning area has been described for red snappers off the Texas and Louisiana coasts. Moe (1963) reported two spawning areas for red snappers off northwestern Florida, which were in waters between 10 and 20 fathoms deep. He reported large catches of red snappers from these areas in July and August. The exact area for spawning in Texas was not located during this study, but might be expected to be similar to that in Florida. Hoese (1965) reported that most marine fish off the Texas coast spawn offshore and that there is an inshore transport of larvae and juvenile stages. Since many small juveniles were found in shallow waters off Port Aransas in September and few adults have been taken in these waters, it is reasonable to predict that the above generalization is true for red snappers. It should be noted that until more collections of ripe adults and series of larvae are made, little information can be added to spawning habits and development of red snappers.

Camber (1955) noted a slight deviation from the 1:1 expected sex ratios, his data indicated that the proportion of males decreased with age, since smaller fish had a higher male ratio while large fish had a higher female ratio. Most of the fish examined in the present study were in the size class of Camber's high male ratio group (200–400 mm) and had a sex ratio of 56% males to 44% females.

## Age and Growth

Although age-growth studies have been conducted on a number of lutjanid fishes, studies of *Lutjanus aya* have been neglected. Pino (1962) found scales to be unsatisfactory for age-growth studies in *Lutjanus synagris* and employed otoliths instead. On the other hand, Croker (1962) was successful in using scales for age-growth studies of *L. griseus*. Talbot (1960) used scales in determining age groups of *L. bohar*, but his data are in conflict with length-frequency studies by Wheeler and Ommanney (1953). Thus, scale validity in this species is questionable. Moseley (1964) found that scales have potential use in age-growth studies of *Pristipomoides andersoni* and that further study was needed to confirm their applicability.

The factors determining the production of growth checks in fish scales are varied. Seasonal migration, spawning, environmental changes, or seasonal food availability could produce growth checks of fish in the Gulf of Mexico. Since monthly samples of scales were not taken throughout the year, it was difficult to determine the exact time growth checks were produced on red snapper scales. Distance of growth rings from the periphery of the scales of fish collected in June and February varied, but most of the checks from the June collection were farther from the periphery than those collected in February. New checks were noted in scale samples from a few fish collected in June, indicating growth ring production in late spring or early summer. Since these growth rings were not produced during the season in which annuli are usually produced (winter), but rather correlates with the spawning season, it may be assumed that spawning is a causal factor in the production of growth rings. This assumption is further supported by Camber (1955) who suggested that red snappers do not feed during their spawning period.

Red snapper age-growth data are presented in Fig. 2. Data from the present study indicate that *Lutjanus aya* have an average standard length of 250 mm for spawning class I. Spawning class 0 average about 100 mm and is not distinctly bimodal, indicating most yearlings spawn. The slight skew above 200 mm may represent the nonreproductive yearlings. Since it is assumed that the growth rings were produced during the spawning season, and most fish were taken in the winter, the size groupings are of fish approximately ½ year older than recorded. Data presented in Fig. 2 indicate red snappers grow approximately 90 mm between spawnings at least up to the fourth spawning period. Based on this growth rate, red snappers probably grow 200 to 220 mm during their first year, although more data is needed to confirm this.

As was suggested earlier, not all red snappers spawn their first year. If the production of growth rings is caused by spawning, it is probable that growth rings do not appear on some fish until their second year. This may explain the high degree of overlap of length frequencies and age classes (Fig. 2).

Growth data from tag returns of red snappers off the Florida coast (Beaumariage,

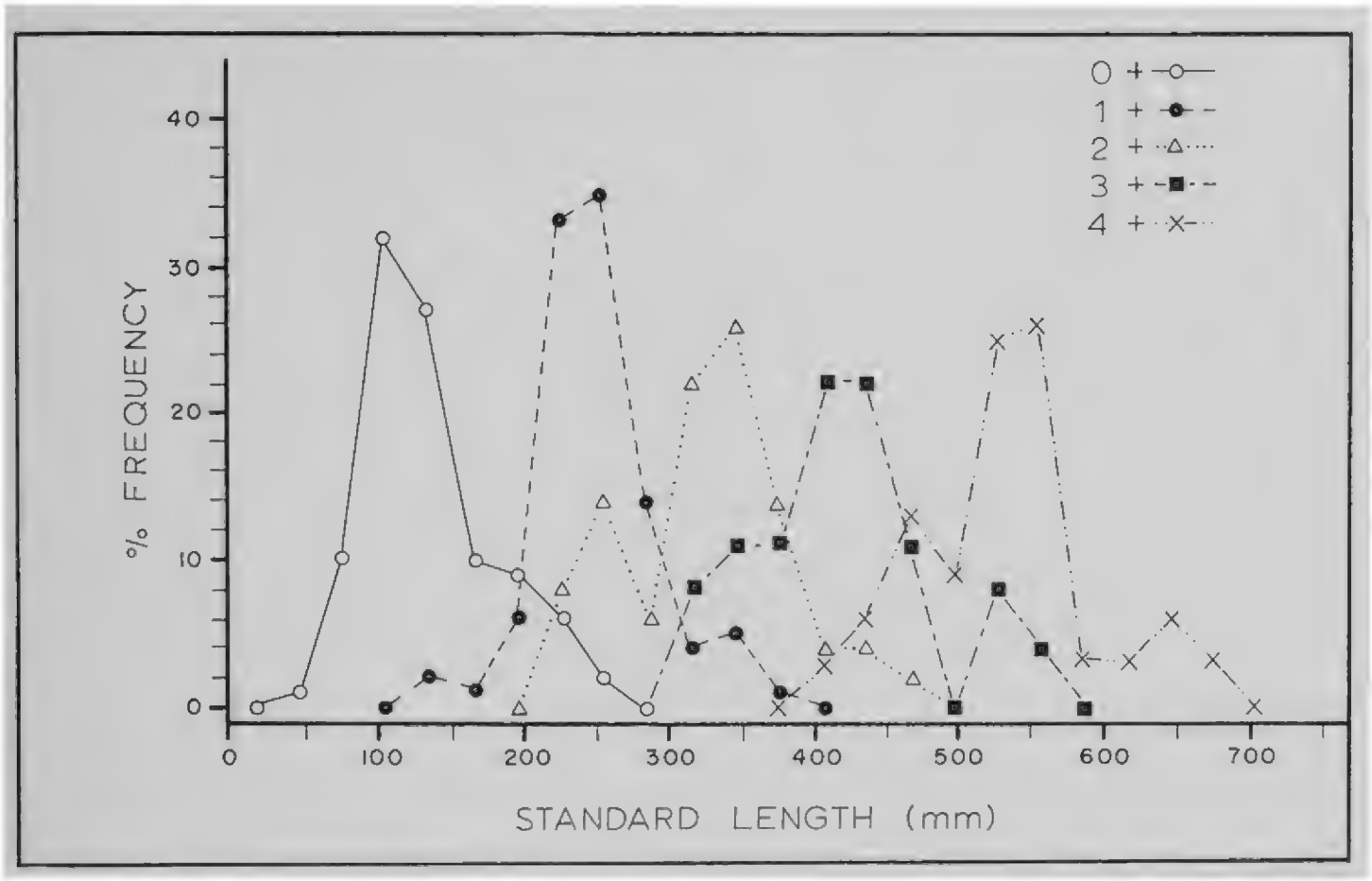


FIG. 2. Length-frequency Distribution of Spawning Classes of Red Snappers. These length-frequency distribution curves are based on 343 snappers; with 87 in the $0^+$, 146 in the $1^+$, 51 in the $2^+$, 27 in the $3^+$, and 32 in the $4^+$ spawning groups.

1964) indicated that red snappers between 250 and 400 mm grew about 80 mm per year. This growth rate supports growth data of the present study, which indicated similar growth rates for spawning classes I, II, and III (Fig. 2). Too few samples were available for growth-rate determinations of spawning classes IV through VI.

Data other than scale readings indicated an accelerated growth during the first year. Juveniles collected in September averaged 49 mm standard length, while those in October averaged 75 mm. Thus, red snappers 50 mm standard length increased their length by ½ in one month. No juvenile snappers were collected from Texas after October 1964, but juveniles collected off Louisiana in February 1964 averaged 130 mm standard length. Although these fish were taken from different areas and after different spawning seasons some correlation of growth could be made.

This growth rate is supported by the fact that few fish at lengths of 130–140 mm and 170 to 210 mm were encountered during the study. No juveniles were collected in the late fall, early winter, spring or early summer. According to the proposed growth rate, fish of these sizes would be expected if collections had been successful during these seasons.

Camber (1955) and Dawson (1963), in studies of length-weight relationships of red snappers, found that the condition factor c was smaller in the fish from 90 to 190 mm than in fish of larger sizes. This was based on the formula $W = cL^n$, where W = weight, L = length and c and n are constants. A sudden change of the c value occurred at lengths from 190 to 300 mm, and was probably due to attainment of sexual maturity. Lagler (1952) reported that changes in the c value are due to changes of form or increases in specific gravity. Dawson (1963) stated that casual observations of red snappers suggest that there is a significant proportional increase in both body depth and

girth of larger red snappers. Data from the present study do not indicate proportional changes in body depth (Fig. 3) with lengths at the appropriate sizes. Body girth-standard length relationship was the same as that for body depth.

## Food Habits

Eversion of stomachs of ascending fish due to decreasing pressure, has long plagued food studies of the red snapper. Stearns (1884) noted the problem in a study in which 450 specimens were examined and food was found in only one. The problem was also encountered by Adams and Kendall (1891) and Camber (1955). My study was no exception; of 712 fish examined for food contents, 375 had everted their stomachs, 160 were empty, and 187 contained food material (Table 1). Eversion was not a problem for samples taken shallower than 20 fathoms; however, data from deeper samples may have been distorted by this problem, because the everted stomachs may have contained different quantities of items of food than the non-everted stomachs used for examination. Attempts to prevent everting, by slowly raising the fish were only partly successful. In some cases this method cut down the efficiency of fishing and did not appreciably decrease the percentage of everting. An example of this type of experiment are the results obtained from Sebree Bank (23 fathoms). As ascent of 5 minutes was successful only 30 to 40% of the time and the fishing time for each haul was tripled.

Results of this study indicated that the red snapper is polyphagous (Fig. 4), in that they ate most anything that was readily available. As indicated in the figure, this was true for both adult and juvenile snappers.

Adult red snappers are primarily piscivorous, although they utilized a great variety of invertebrates. Utilization of tunicates was important, as results show that when they

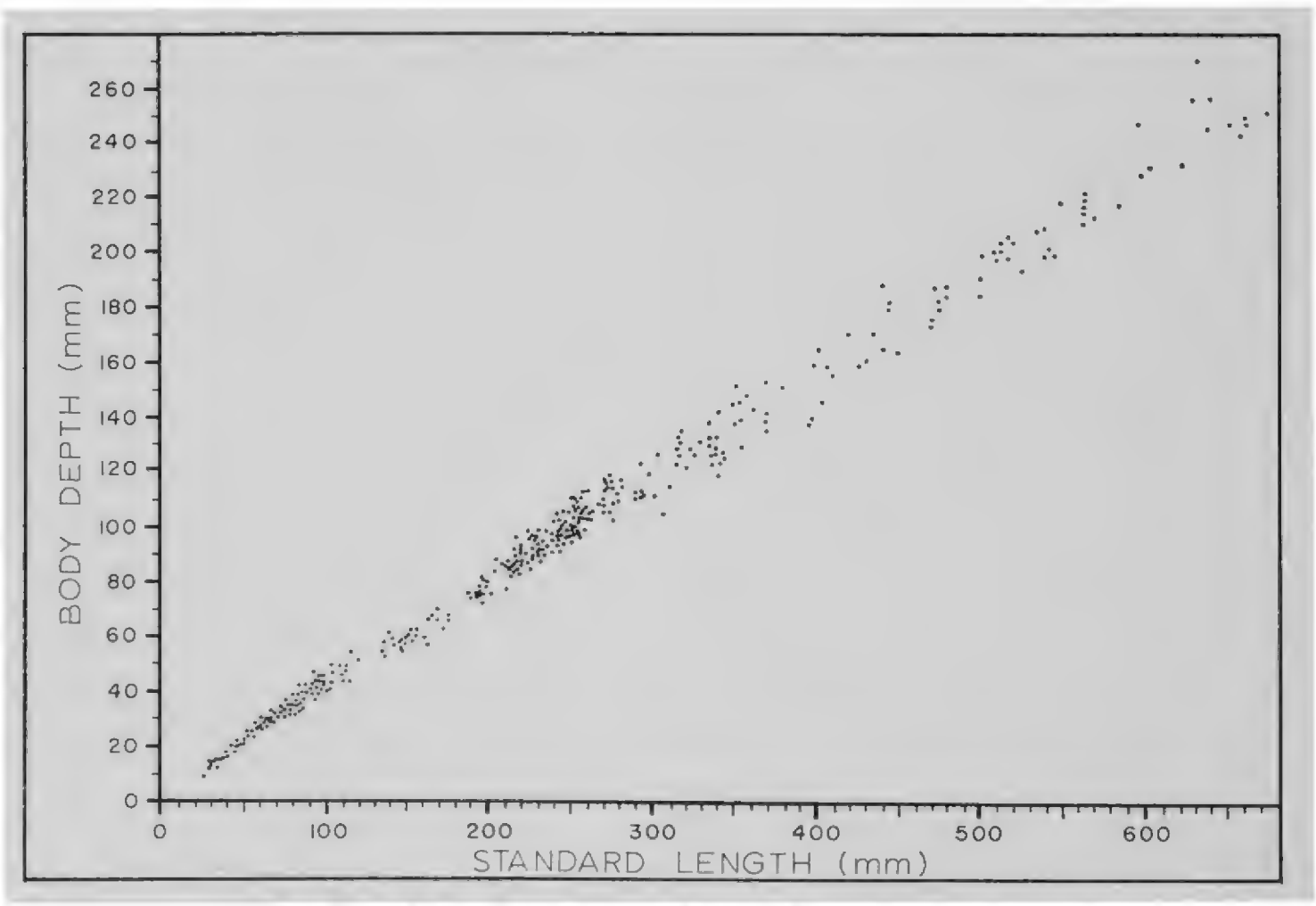


Fig. 3. Body Depth vs. Standard Length of 487 Red Snappers.

TABLE 1

Stomach Eversion Comparison with Depth and Gear

| Depth | Number Fish | Number Everted | Number Empty | Number With Food |
|---|---|---|---|---|
| | | Taken by Handline | | |
| 7½ f | 56 | 0 (0)[a] | 23 (40) | 33 (60) |
| 23 f | 213 | 189 (89) | 13 (6) | 11 (5) |
| 31 f | 43 | 34 (79) | 8 (19) | 1 (2) |
| 32 f | 100 | 65 (65) | 12 (12) | 23 (23) |
| 33 f | 100 | 37 (37) | 18 (18) | 45 (45) |
| | | Taken by Trawl | | |
| 7–9 f | 42 | 1 (2) | 18 (43) | 23 (55) |
| 15–16 f | 28 | 1 (3) | 12 (43) | 15 (54) |
| 18–21 f | 27 | 2 (7) | 18 (67) | 7 (26) |
| 24–25 f | 37 | 6 (16) | 18 (49) | 13 (35) |
| 30–31 f | 48 | 31 (64) | 9 (19) | 8 (17) |
| 39 f | 17 | 9 (53) | 1 (6) | 7 (41) |

[a] ( ) = Percent

were a part of the diet they constituted about 50% of the food taken. Evidently tunicates are taken when they are most abundant. Camber (1955) reported that a tunicate, *Clavelina* sp., was often taken by red snappers during the spring off the Florida coast. This seasonal utilization corresponds to the heavy predation of the colonies of *Distaplia* off the Texas coast in June (Fig. 4 B). This tunicate is often referred to as "Tapioka" by local fishermen, just as *Clavelina* is in Florida (Camber, 1955). Another tunicate, *Salpa confederata*, was common in the diet of red snappers taken from "Lump 33" off the Louisiana coast (Fig. 4 A). Since *S. confederata* is free-swimming and pelagic, it probably

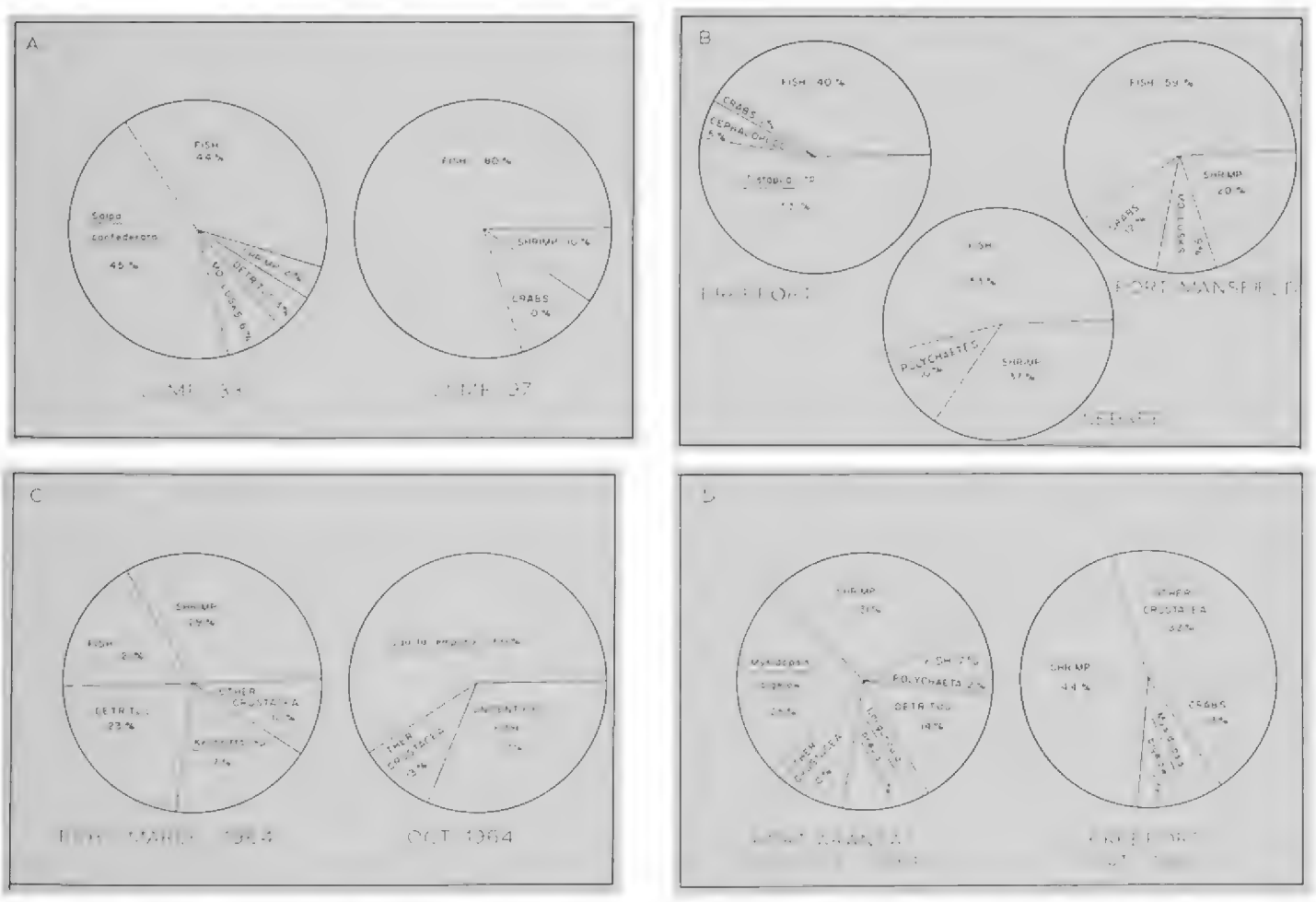


FIG. 4. Food Habits of Red Snappers by Volume. A. Louisiana Adult Red Snappers. (46 Stomachs); B. Texas Adult Red Snappers. (68 Stomachs); C. Louisiana Juvenile Red Snappers. (28 Stomachs); D. Texas Juvenile Red Snappers. (45 Stomachs).

was not taken from the bottom as was the colonial *Distaplia*. *S. confederata* was found only in this one area and not found in those fish sampled on "Lump 97" four days earlier. It is therefore assumed that this was a local concentration.

More evidence of predation on readily available food is indicated by the larger concentration of shallow-water crabs and shrimp in snappers 7½ fathoms off Port Mansfield than in samples from further offshore.

Some of the food items in snapper stomachs indicated that they do not always feed on reef forms. Hildebrand (1954) reported that *Hoplunnis macrurus* (found in Louisiana snapper stomachs) was very common on the brown shrimp grounds off Texas and Louisiana, but did not report them in his (1955) study of the more rocky Campeche area. These studies indicate that *H. macrurus* prefers mud or sand bottom, and that the specimens taken off Louisiana probably came from this type of habitat (Moseley 1965). The small gastropods, *Sinum perspectivium*, which were found in snappers taken from shallow waters off Port Mansfield, also have a preference for sandy or muddy bottoms (Rehder, 1954). Other food items showing preference for similar habitats are *Penaeus aztecus*, *Trachypeneus* and *Sicyonia* (Hildebrand, 1954). This is especially true for *Penaeus aztecus*, which buries in the mud during daylight. Almost all adult snappers caught off the Texas coast were taken at least several hours after sunrise. Longley and Hildebrand (1941) studying the related *Lutjanus griseus*, found that digestion of shrimp and fish was almost complete in 3½ hours. Therefore, the shrimp were probably dislodged from the mud by the snappers. It is quite possible that many other species may have also been taken in sandy or muddy areas. Therefore, red snappers are probably not as confined to reefs or rocky areas as previously believed. This is further supported by large commercial catches of red snappers in muddy offshore areas (Moe, 1963; personal communication with commercial fishermen). Based on food habits, there seems to be no particular reason why red snappers should congregate on reefs or rocky areas, since the availability of food found in snapper stomachs is probably comparable for mud, sand, and rocky type habitats. The converse is also true, as most motile food items are not necessarily confined to mud and sand.

Juvenile red snapper food habits have not been previously recorded. As mentioned earlier, they are polyphagous, although food emphasis is shifted from fishes to crustaceans (Fig. 4C and 4D). The diet of juveniles can be divided into two different categories: zooplankton (which includes chætognaths and larval crustaceans and fishes), and macro-animals (cephalopods, crabs, juvenile shrimp, and fishes).

In fish between 40 and 90 mm there is a slow transition of diet from a dominance of zooplankton in the diet of smaller fish, to a dominance of macro-animals in the diet of larger. Fishes betweeen 80 and 170 mm appear to feed indiscriminately on whatever is available. This indiscriminate feeding is supported by the fact that fish, ranging between 120 and 160 mm, caught off the Louisiana coast in February and March 1964 fed heavily on larval fish, larval shrimp and arrow worms, *Krohnitta* sp. Occurrence of plankton in lutjanids of this size is not surprising, as Talbot (1960) and Wheeler and Ommanney (1953) found plankton in the diet of *L. bohar*. On the other hand, fish ranging from 70 to 110 mm caught off the Louisiana coast in October 1964 fed heavily on *Squilla* and juvenile macro-animals, presumably because it is inefficient for snappers this large to exist on zooplankton (Fig. 5).

Another instance which illustrated the red snapper's ability to capitalize on avail-

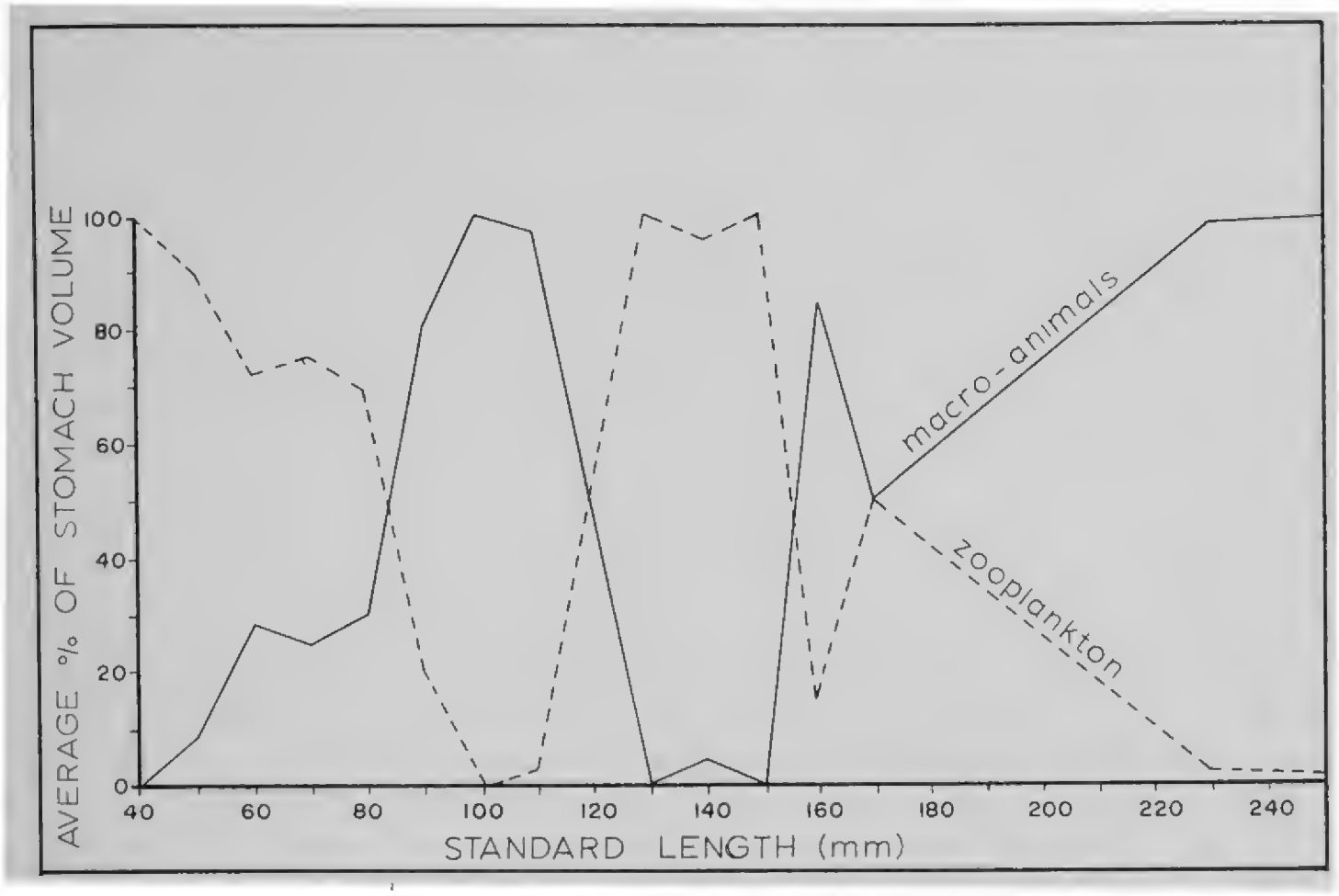


FIG. 5. Ontogenetic Food Progression of Red Snappers.

able food is shown in data taken from 9 fathoms in September 1964 off Port Aransas, where almost 100% of the food content was larval *Mysidopsis bigelowi*. One month later snappers were not found in this area, but in 18 to 24 fathoms and were feeding on small cephalopods, shrimp and fish.

Since no diurnal data were taken, no special feeding times can be delimited for adult snappers. Fishermen, however, have reported snappers biting at certain times in different areas. This theory held true for "Lump 33" and "Lump 97" off Louisiana, because these areas are termed by some as "night lumps." Although these areas were fished in the afternoon, no red snappers were landed until sundown. There was no correlation of the percentage of empty stomachs of those caught at sundown to those caught later. Thus, it is not known whether the snappers suddenly began feeding or if they just moved into the fishing area. Other instances indicate snappers suddenly bite for short periods of time, but this may be due to schools of snappers moving into and out of the fishing areas.

As in the adults, no specific feeding times could be ascertained for juveniles, although data indicated that they feed at night as well as in the daytime. Snappers examined from off the Louisiana coast in October 1964 were sampled at night. The high percentage of *Squilla empusa* (Fig. 4C) correlates with night feeeding, because *Squilla* usually burrow in the day and come out at night (personal observation).

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# Movement of Radioisotopes in a Marine Bay: Cobalt-60, Iron-59, Manganese-54, Zinc-65, Sodium-22[1]

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## Abstract

Cobalt-60 tracer experiments indicate that a small highly mobile pool of cobalt exists in a bay bottom community dominated by the marine grass, *Thalassia testudinum*. The cobalt-60 content of the grass around midnight was about five times the noon value. Indirect evidence points to the sediment as the other half of the cycle. Either surface adsorption or metabolic activity by the *Thalassia* and/or the variety of algae which the *Thalassia* bears as epiphytes on the blades are possible uptake mechanisms. Similar experiments were conducted using iron-59, manganese-54, zinc-65 and sodium-22.

In order to gain some insight as to the pathway and rate of movement of trace metals in a marine bay, radioactive isotopes were used as a tracer. A thick bed of *Thalassia testudinum* growing in Redfish Bay near Port Aransas, Texas, was the site of the experiments. These grass beds are very productive in terms of oxygen production (Odum and Wilson, 1962), so it was hoped that they would show a rapid trace metal movement. A standard experiment was developed so that runs with different radioactive tracers could be compared.

A polyethylene cylinder (45.7 cm diameter, 155 cm length) sunk into the sediment in a *Thalassia* bed isolated a known area for study. The water depth was about 30 cm, with no exchange of water between the inside and outside of the cylinder. Small battery powered cocktail stirrers slowly mixed the water column. A known activity of the appropriate carrier-free radioisotope was poured into the water and periodic sampling performed according to a prearranged schedule. An old breakfast table sunk a few inches into the sediment beside the cylinder served as a field laboratory. Duplicate samples of water (4 ml) and of grass (0.2 g) blade were taken in marked and weighed test tubes. It was found that the sediment could not be sampled without stirring up a cloud of fine mud which ruined the experiment. Therefore only an occasional sample of sediment was taken near the end of an experiment. At the end of the sampling period the test tubes were taken to the laboratory, dried (75 C for the grass), weighed and counted. Activity measurements were made using a Nuclear Chicago single channel gamma spectrometer with a well-type NaI crystal. The samples were corrected for background and the results recorded as counts per minte per ml for water or per gram for grass.

This experiment was carried out twice for each element. Typical results are presented in Figs. 1 and 2. All the trace metal experiments yielded results which are similar in several respects: (1) the activity of the water quickly fell to a low value and remained

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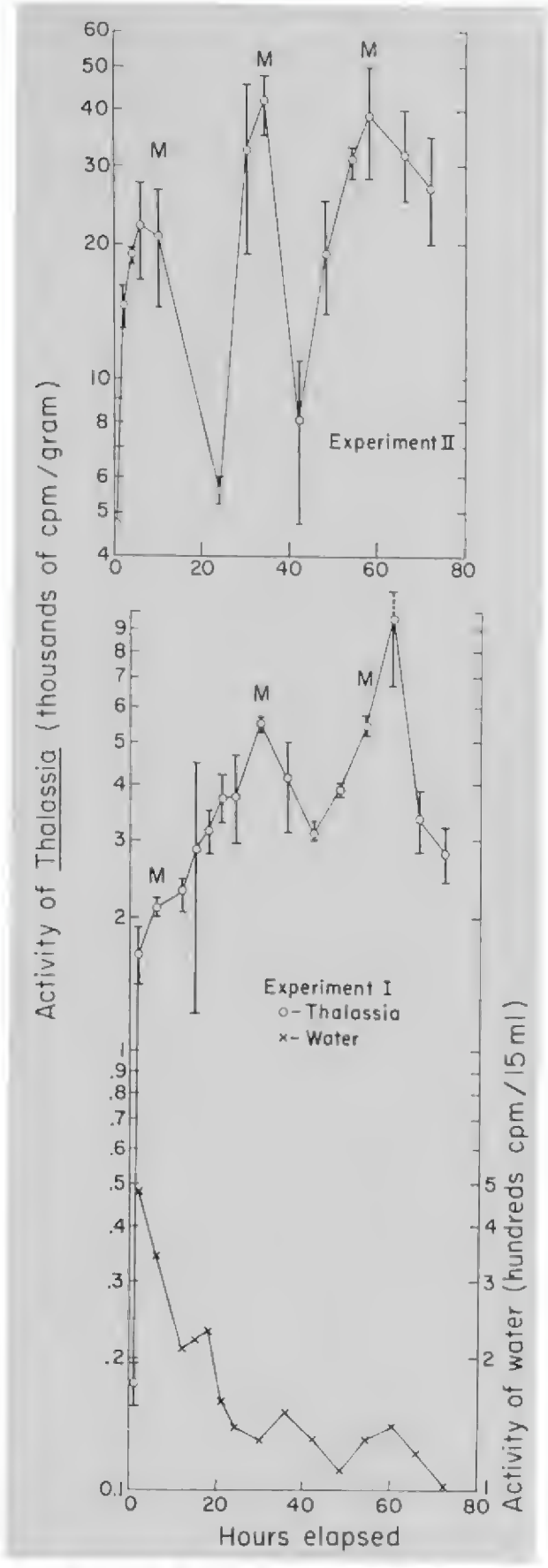
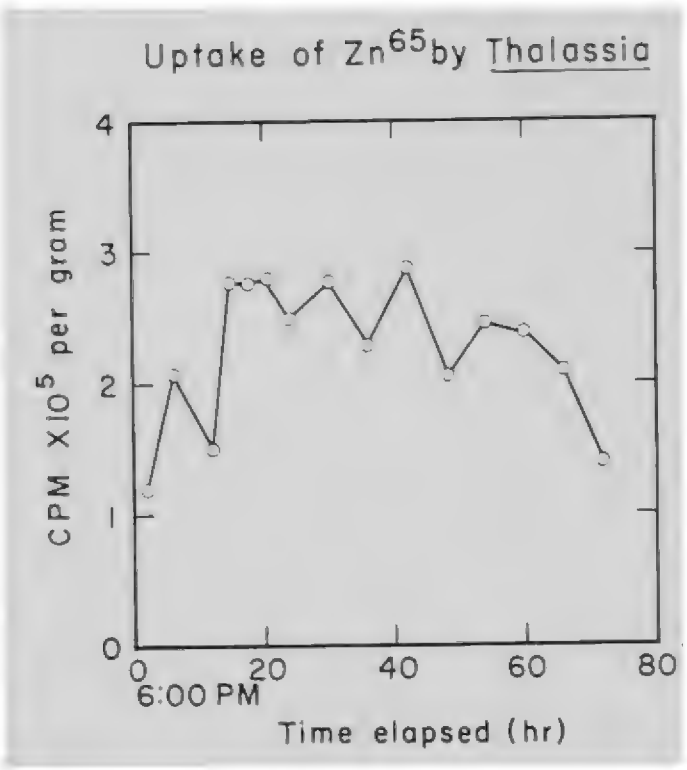
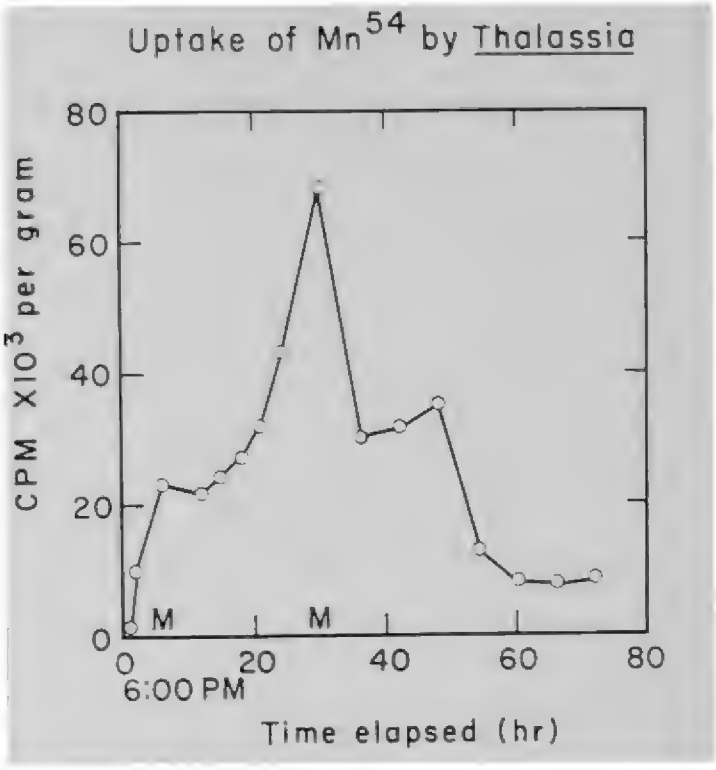


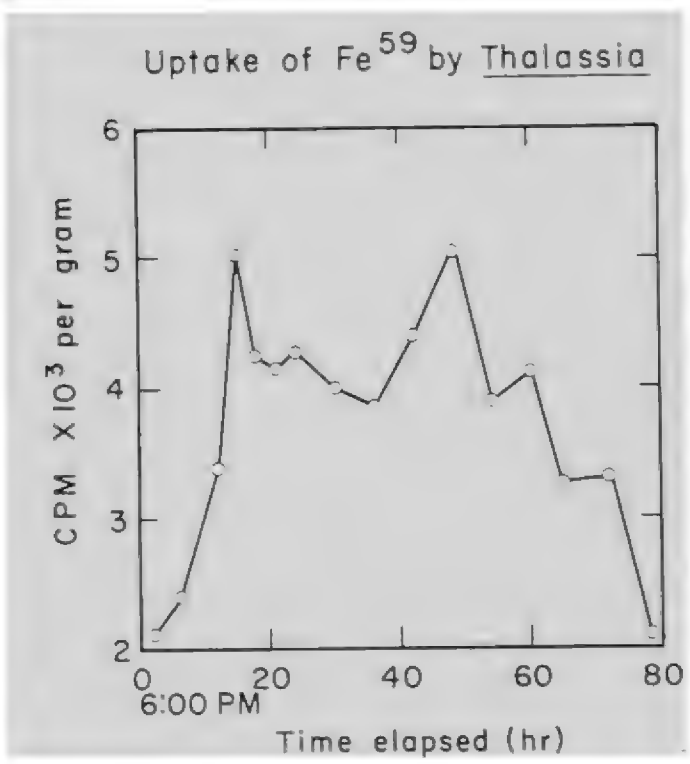

FIG. 1. Duplicate experiments showing the uptake of Co-60 by *Thalassia*. Only experiment I shows the loss of activity by the water which was observed in both.

fairly constant, (2) the grass quickly took up the tracer then later released part of it, and (3) most of the radioactivity eventually appeared in the sediment. As expected, the sodium-22 results were different. There was essentially no uptake by the *Thalassia*, as most of the tracer remained in the water.

A further observation concerns the distribution of the tracer between the roots and blades of *Thalassia*. The results of a series of the standard experiments designed to show this relationship are shown in Table 1. For the elements tested, manganese, cobalt,



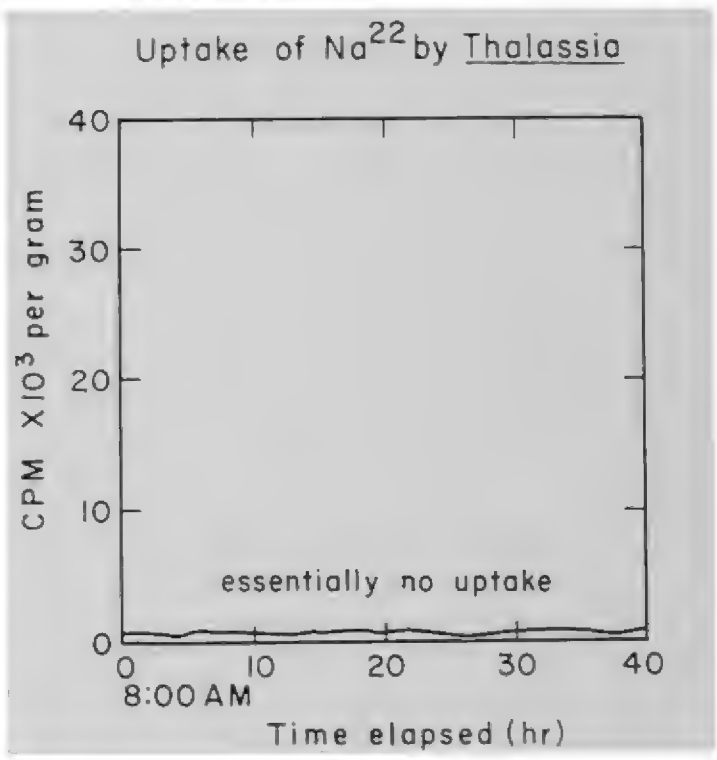




FIG. 2. Typical experiments showing the uptake of Zn-65, Mn-54, Fe-59 and Na-22 by *Thalassia*.

and zinc, the roots took up a small but significant fraction of the tracer. This concentration of tracer in the blades and near absence in the roots is evidence that the mechanism of uptake is adsorption by the *Thalassia* blades or uptake by the variety of algae which the blades bear as epiphytes.

Yousef and Gloyna (1964) reported on an extensive investigation of the transport of Co-58 in a plume modeled after a river. Several of their observations were similar to those made in this work and it seems worthwhile to tabulate them.

(1) In both cases the plants showed rapid uptake with slow loss to the sediment.
(2) In both cases the tracer did not penetrate the sediment more than one or two cm.
(3) The tracer was highly concentrated in the leaves of the plants with respect to the roots.

TABLE 1

Activity of Blades and Roots[a] of *Thalassia*

| Time Sampled Hrs. | Co-60 Activity[b] of Blades × $10^3$ | Co-60 Activity of Roots | Mn-54 Activity of Blades | Mn-54 Activity of Roots |
|---|---|---|---|---|
| 0 | 300 | 69 | 2350 | 62 |
| 24 | 120 | 12 | 2630 | 86 |
| 48 | 120 | 17 | 1949 | 137 |
| 72 | 70 | 36 | 2951 | 12 |
| 144 | 90 | 22 | 358 | 17 |
| 168 | 110 | 57 | 827 | 29 |
| 192 | 110 | 41 | 1410 | 14 |

| Time Sampled Hrs. | Zn-65 Activity of Blades | Zn-65 Activity of Roots | | |
|---|---|---|---|---|
| 0 | 4409 | 416 | ..... | .... |
| 24 | 5606 | 937 | ..... | .... |
| 48 | 5050 | 131 | ..... | .... |
| 72 | 5700 | 66 | ..... | .... |
| 144 | 12400 | 74 | ..... | .... |
| 168 | 8890 | 156 | ..... | .... |
| 192 | 18600 | 229 | ..... | .... |

[a] Samples were taken at noon each day.
[b] Average of duplicate samples in cpm per gram for data.

(4) For the fresh water system the tracer remained in the water longer than in the marine system in which the sediment and plants quickly concentrate the tracer.

In the *Thalassia* community the grass and the sediment dominate the trace metal biogeochemistry. From time to time small animals and bits of large algæ were found in the tanks and checked for radioactivity. These traces of radioactivity did not influence the overall material balance. The grass and sediment contain most of the inventory of trace metal in the grass flat system (Parker, 1962; Parker, Gibbs and Lawler, 1963). Therefore the tracer experiments can be regarded as the result of the gradual isotopic equilibration of the added tracer elements with the various stable pools already present except that the time scale was not long enough for the roots to exchange. The time involved for this process is a qualitative measure of the normal rate of biogeochemical turnover of the element. For the elements studied, a time scale of hours is indicated by the rapid fluctuations shown in Figs. 1 and 2.

Cobalt is one of the least abundant trace metals in marine environments (Goldberg, 1965). Biologically it is one of the most important trace elements (Lowman, 1963). Both of these conditions hold for *Thalassia* grass flats (Parker *et al.*, 1963). For these reasons more work was done with cobalt-60 than with other tracers. These results were unusual and interesting and will be discussed in some detail. However, it is only fair to point out that severe problems exist in a field experiment such as this, especially in sampling.

The results of two independent experiments on the cobalt-60—*Thalassia* system are shown in Fig. 1. In both experiments the activity of the water decreased steadily with time. Experiment II shows three maximum points of cobalt-60 uptake all very close to midnight. Experiment I shows the same maxima but the first minimum is missing due to the great spread between duplicates in point four. The average spread between duplicate samples is 16 percent of the value plotted in Experiment I and 23 percent in Ex-

periment II. The spread is attributed to inhomogeniety in the randomly sampled grass blades. One could see that some blades were young shoots while others were old and well coated with algæ.

Indirect evidence indicates that the sediment is the other half of the observed diurnal cycle. At the end of Experiment I the sediment contained 37% of the added tracers. After the first few hours the water did not contain more than 10% of the total tracers. Thus the sediment is the only thing left. It is very interesting that the roots of the *Thalassia* took up less than 1 percent of the total tracer although it accounted for 90 percent of the biomass of the system. Table 2 gives a slightly idealized material balance for Experiment II. There is not a material balance at every time because data on the sediment activity is lacking.

A relation between uptake of trace and light intensity has been noted by Bachmann and Odum (1960). They reported uptake of zinc-65 by six species of marine benthic algæ in proportion to the gross oxygen production. In their experiments a single species of algæ was suspended in a bottle and the loss of tracer from the water noted. Bruce and Hood (1959) observed a diurnal variation in dissolved phosphate in the water over a *Thalassia* community. Thus there is some rationale for the idea that other elements, especially those in short supply, might show diurnal variations like oxygen and "P" carbon.

Finally, one should bear in mind that sediment includes the many algæ and bacteria that live in the upper part of the mud. Thus if there is a coupled movement of cobalt it is probably between two living groups.

TABLE 2

Material Balance of Co-60 in Experiment II

| | | |
|---|---|---|
| I. Description of System at time zero. | | |
| Volume of sea water | = | $4 \times 10^4$ ml |
| Weight of grass blades | = | 20 g |
| Weight of grass roots | = | 270 g |
| Area of sediment | = | 800 $cm^2$ |
| Total activity added | = | $3 \times 10^6$ cpm |
| II. Distribution of Co-60 after ½ hour. | | |
| Total water activity | = | $1.6 \times 10^6$ cpm |
| Total grass blade activity | = | $5.4 \times 10^4$ cpm |
| Total grass root activity | = | $2.3 \times 10^4$ cpm |
| Total sediment activity | = | $1.1 \times 10^6$ cpm |
| Total activity of tank | | $2.8 \times 10^6$ |
| III. Distribution of Co-60 after 24 hours (a minimum in grass uptake) | | |
| Total water activity | = | $2.4 \times 10^5$ cpm |
| Total grass blade activity | = | $1.1 \times 10^5$ cpm |
| Total grass activity | = | $2.3 \times 10^4$ cpm |
| Total sediment activity | = | $1.1 \times 10^6$ cpm |
| Total activity of tank | | $1.4 \times 10^6$ |
| IV. Distribution of Co-60 after 34 hours (a maximum in grass uptake) | | |
| Total water activity | = | $1.6 \times 10^5$ cpm |
| Total grass blade activity | = | $8.3 \times 10^5$ cpm |
| Total grass root activity | = | $2.3 \times 10^4$ cpm |
| Total sediment activity | = | $1.1 \times 10^6$ cpm |
| Total activity of tank | | $2.1 \times 10^6$ |
| V. Explanations of numbers used in these calculations. | | |

The activities of the grass blades and water were the measured values for the time in question.

The activity used for the sediment is the average of three measurements made on sediment samples taken at the end of the experiment (T = 72 hr.).

The activity used for the grass roots is the average of four measurements made on grass root samples taken at noon on the four days following the end of the experiment. Thus these values represent times when the grass blades were at a minimum in activity.

## Acknowledgments

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# Recent Marine Ostracod Assemblages of Puerto Rico[1]

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## Abstract

Five ecological assemblages of Recent marine octracods have been established for Puerto Rico. The assemblages are based primarily on selected species of ostracods and environmental factors such as sediment type, organic content of the sediment and water depth. Two groups of ostracods, designated as primary and secondary indicators were used to establish the assemblages. Primary indicators, a total of 40 species, include the most abundant species with both live and dead representatives. Secondary indicators of the assemblages, a total of 12 species, included species that were very abundant and occurred in 55% or more of the 116 total samples but had no living representatives. Thus, 52 of the 230 species found off Puerto Rico were useful ecological indicators.

## Introduction

Studies of Recent ostracods in the Caribbean Sea have been relatively sparse. Most of the studies have been taxonomic in nature with little or no ecological data given.

Brady (1866) was one of the first to study the ostracods in the Caribbean. He studied the Ostracoda of Turks Island, Bahamas and the West Indies. Three years later, Brady described several new species from New Providence, Bahamas, Haiti, and the Colon-Espinwall coast of Panama. Some of these species were included in a series of later publications by Brady (1867-1872). Brady (1880) described seven species, five of which were new, from a sample collected off the coast of Culebra, west of Puerto Rico.

Van den Bold (1946) noted the presence of several species, originally described from the Tertiary of the Caribbean, living in the Recent sediments around Cuba. Key (1954) initiated a systematic investigation of the ostracoda of the Gulf of Paria in conjunction with the investigation of the Recent sediment. He reported a total of 38 species.

Tressler (1954) compiled a list of known species from the Gulf of Mexico and the Caribbean, reporting 19 species from the latter. Kornicker in a series of papers (1958, 1959, 1961, 1963) reported on the ecology, distribution and taxonomy of the ostracods of the Bimini area of the Great Bahama Bank. Van den Bold (1963a) described the hinge structure of a new species of *Cytherelloidea* collected from Pidgeon Point, Tobago. Van den Bold (1963b) revised the systematics of *Orionina* using both paleontological and Recent material from the Gulf of Mexico and the Caribbean. He also reported (1963c) numerous species from the Miocene and Pliocene deposits of Trinidad that have living representatives in present-day environments.

Benson and Coleman (1963) in a paper dealing primarily with Gulf of Mexico ostracods suggested three biogeographic realms including a Caribbean realm.

[1] Based on part of a thesis submitted by the first author in partial fulfillment of the requirements for the degree of Master of Science at Texas Christian University, Fort Worth.

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## Oceanography of Puerto Rico

Puerto Rico is the most easterly of the Greater Antilles Island, situated between 17° 50′ and 18° 30′ N. and 65° 30′ and 67° 15′ W., therefore, within the tropical zone. Puerto Rico is bounded on the south by the Caribbean Sea and on the north by the Atlantic Ocean. The island is rectangular in shape, about 100 miles long and 40 miles wide.

The island is surrounded by a narrow shelf which is widest on the east coast where it extends to the other islands of the Antilles chain, and the narrowest on the west coast near Punta Rincon where it is but a thousand yards wide (Almy and Carrion-Torres, 1963).

Currents of Puerto Rico are dominated by the northwesterly drift of the North Equatorial current (Kaye, 1959). Coastal currents on the north and south coasts are generally in a westerly direction, but the flow tends to be northerly on the east and west coasts. Kaye (1959) remarked that reversals of flow occasionally occur as a result of tides and other undetermined factors. According to Wüst (1964) the velocity of the surface currents is relatively constant. Almy and Carrion-Torres (1963) pointed out that the north and east coasts are subject to much greater wind and wave action than the south and west coasts except during periods of major storms.

Wüst (1964) stated that the annual surface salinity range around the island is 34.6 to 35.9 ppt. At a depth of 200 m, the annual range is 34.5 to 36.5 ppt. Kaye (1959), however, pointed out that the south coast has slightly lower salinities than waters of the other areas. Kaye's explanation of this phenomenon is that the persistence of dilution by land drainage on the rather shoal and relatively calm south coast may be of greater effect than on the rather rough north coast even though runoff is greater on the latter.

As expected in tropical seas, water temperatures are relatively high, ranging from 28 C in March to 30 C in September (Kaye, 1959). Wüst (1964) reported a surface difference of about 2.7 C between the warmest month (28.3 C) and the coldest month (25.6 C). The temperature at 200 m is around 20 C according to Wüst (1964).

## Method and Materials

During the summer of 1963, a total of 116 qualitative bottom samples were collected jointly off the coast of Puerto Rico by Dr. Dan E. Feray and the junior author, for biological studies. The locations of all sample localities and transects are shown in Fig. 1. Two types of sampling devices were used to collect the samples. One, the Peterson grab, was found not to be very reliable, especially in deep water. The other device, a "bucket" constructed from steel casing ten inches in diameter and 18 inches long, proved to be more reliable. The bucket was pulled along the bottom for a variable length of time.

Fifteen transects, perpendicular to the coasts, were sampled around the island. Sediment samples were taken at selected depths of 10, 25, 50, 75, 100, 300 and 600 feet. In some cases, additional depths were sampled and in other cases certain of the above depths were not. Twenty-two localities other than the transects were also sampled. Each sample collected from the transects was denoted by a letter and a number. The non-transect samples were designated by two digit numbers and in some cases letters.

A representative cut of the original sample was taken and preserved in 5% neutralized sea water formalin. The volume of the cut varied but usually was about one pint. Surface and bottom water samples were taken at a few of the sampling localities.

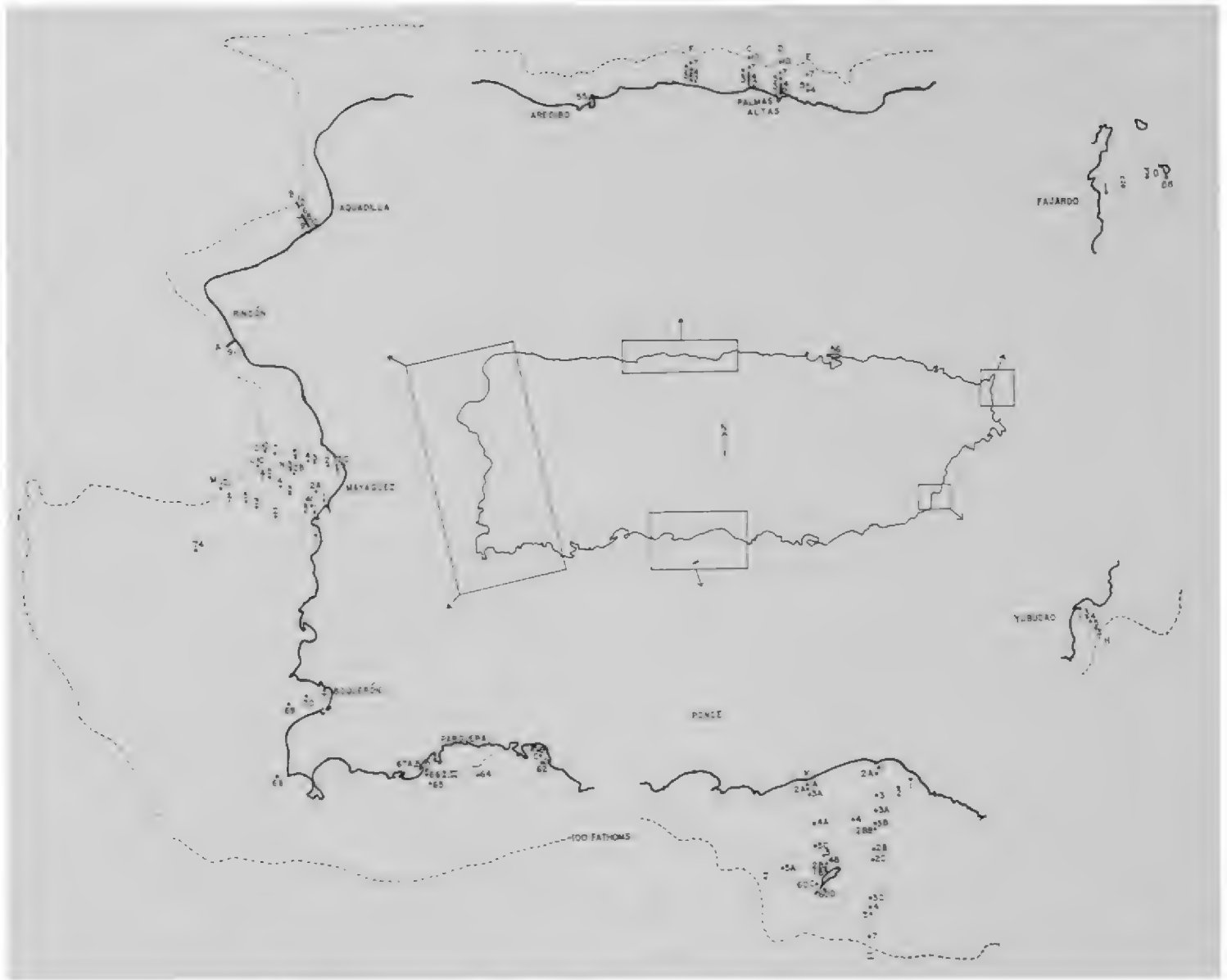


FIG. 1. Location of sampling stations around Puerto Rico.

In the laboratory, a representative cut was taken from each preserved sample for ostracods. The cut was usually 100 ml, but in some cases, 25 ml cuts (samples F-3, H-3, H-9) or 50 ml cuts (samples A-8, A-9, B-1, B-8, J-5a) were taken because of the small volume of sediment available. For six samples (B-7, I-4, I-7, M-10, N-3) no cuts were taken because of the very small volume; therefore, the entire sample was used.

The chlorinity of the sea water was determined by the standard Knudsen method; *i.e.*, titrating with standardized silver nitrate. Chlorinity then was converted to salinity. The organic carbon montent of the sediments was determined by the Schollenberger (1931) chromic acid reduction method using the refinements of Allison (1935). The Schollenberger method gives organic carbon only, since elemental carbon is not oxidized. This method does not permit a complete determination of organic content since only organic carbon is determined.

The sediment type was determined by using a modified settling method. A 0.5 inch core was taken from each preserved sample to insure a representative sample. The core of sediment was then placed in a test tube, water was added to make a total volume of two-thirds the height of the test tube, and the tube was then shaken and the contents allowed to settle for at least 24 hours. The height of the entire column of sediment was then measured and the percentage of mud, (including the silt and clay fractions), sand or gravel was calculated. It must be emphasized that the sediment types were determined visually by grain size and not composition. After calculation, the sediment type was

designated as follows: mud—greater than 80% mud; sandy-mud—50 to 80% mud, the rest sand; sand and mud—50% sand and 50% mud; muddy sand—50 to 80% sand, the rest mud; sand—greater than 80% sand; mud-sand gravel—highest % gravel with sand and mud present; gravelly sand—50 to 80% sand, the rest gravel; sandy gravel—50 to 80% gravel, the rest sand; gravel—greater than 80% gravel. Table 1 summarizes the salinity, organic carbon, sediment type and depth for each station.

## Results and Discussion

### *Ostracod Assemblages of Puerto Rico*

Various authors have proposed assemblages of ostracods on a wide variety of criteria. The criteria utilized range from the use of only live individuals to the use of live and dead and finally to the use of only dead individuals. When possible, only live individuals should be correlated with ecological data since dead valves are susceptible to transport by currents, and, therefore, may produce a false image of their true distribution. In some cases, both live and dead individuals are used with the environmental limits established on the basis of the living as is done in this paper. Additional criteria include the use of various environmental factors such as salinity, temperature, water depth, oxygen concentration, sediment type, and organic content. Ideally, one should have a measure of all of these factors to properly interpret their significance in distributions.

A total of 218 species of podocopid and 12 species of myodocopid ostracods were classified from the samples collected around Puerto Rico. Only selected podocopid species, however, were utilized in defining the ecological assemblages. The more abundant species with both live and dead representatives, a total of 40, were designated as primary indicators. Secondary indicators, 12 species, included species with only dead representatives but were very abundant and occurred in 55 percent or more of the total samples.

Distribution of the assemblages is correlated primarily with sediment type, organic carbon content and depth. Additional factors such as physical energy, currents, and topography, which are interrelated, are interpreted as playing a role in distribution. No data are available on salinity and temperature to permit evaluation. These factors are not considered as significant in controlling the distribution of ostracods because of their constancy. The total ostracod fauna can, however, be considered a high salinity and warm temperature fauna.

The assemblages proposed are ecological assemblages, that is, all members appear to have essentially the same broad environmental requirements. There is no implication of interrelationships between the species of a given assemblage.

Two additional conditions should be pointed out regarding the assemblages. First, some of the assemblages overlap. Within areas of overlap, however, the assemblages occupy an environment in which a particular set of environmental conditions are present. Second, the sampling was concentrated in certain areas around Puerto Rico. It is assumed that the assemblages would occur in areas not sampled especially if the same indicator species were found at two or more different sampling areas.

Assemblage A—Eighteen species are included in this assemblage as follows:

Primary Indicators

*Bairdia antillea* van den Bold

TABLE 1

Hydrographic Data for the Stations

| Sample | Salinity (ppt) surface | bottom | Organic carbon (%) | Sediment type | Depth (ft.) | Sample | Salinity (ppt) surface | bottom | Organic carbon (%) | Sediment type | Depth (ft.) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A-1 | 37.14 | ..... | .32 | Sand | 10 | J-4 | 35.70 | ..... | 1.12 | Sandy Mud | 75 |
| A-2 | 35.84 | ..... | .51 | Muddy Sand | 25 | J-5A | | ..... | ..... | Gravelly Sand | 100 |
| A-3 | 35.88 | ..... | .25 | Sand | 50 | J-5C | 35.77 | ..... | ..... | Mud | 100 |
| A-4 | 36.04 | ..... | .59 | Muddy Sand | 75 | | | | | | |
| A-5 | 35.95 | ..... | .63 | Muddy Sand | 100 | K-1A | 35.64 | 35.66 | .43 | Sand | 10 |
| A-6 | 37.39 | ..... | .54 | Muddy Sand | 200 | K-1B | 35.70 | 35.71 | .41 | Sand | 10 |
| A-7 | ..... | ..... | ..... | Muddy Sand | 300 | K-2A | 35.70 | 35.66 | .58 | Muddy Sand | 25 |
| A-8 | ..... | ..... | ..... | Muddy Sand | 400 | K-2B | | ..... | .75 | Sandy Mud | 25 |
| A-9 | ..... | ..... | ..... | Sandy Mud | 500 | K-3A | 35.73 | ..... | .95 | Sandy Mud | 50 |
| | | | | | | K-4A | 35.77 | ..... | .99 | Sandy Mud | 75 |
| B-1 | ..... | ..... | ..... | Muddy Sand | 600 | K-4B | ..... | ..... | .70 | Sand and Mud | 75 |
| B-2 | ..... | ..... | .82 | Sandy Mud | 500 | K-5 | 35.71 | ..... | 1.23 | Mud | 100 |
| B-6 | 35.95 | ..... | 1.10 | Sand and Mud | 100 | | | | | | |
| B-7 | 35.86 | ..... | ..... | Sand | 75 | L-1 | 34.54 | 35.14 | .61 | Muddy Sand | 10 |
| B-8 | 35.77 | ..... | 2.19 | Sand | 50 | L-2 | 35.16 | 35.23 | 1.06 | Sand and Mud | 25 |
| B-9 | 35.88 | ..... | .33 | Muddy Sand | 25 | L-3 | 36.56 | 35.41 | ..... | Muddy Sand | 50 |
| B-10 | 37.19 | ..... | 1.59 | Sandy Mud | 10 | L-4 | 36.69 | 36.85 | .48 | Sand | 75 |
| | | | | | | L-5 | 35.23 | 35.75 | .60 | Sand | 100 |
| C-2 | ..... | ..... | 1.21 | Muddy Sand | 25 | L-7 | 35.57 | ..... | 1.24 | Sand | 300 |
| C-3 | ..... | ..... | .35 | Muddy Sand | 50 | L-10 | 35.30 | ..... | .85 | Sandy Mud | 600 |
| C-4 | ..... | ..... | .35 | Sandy Mud | 75 | | | | | | |
| C-5 | ..... | ..... | .59 | Sand | 100 | M-1 | 36.64 | 35.14 | 1.34 | Sand | 10 |
| C-7 | ..... | ..... | .69 | Muddy Sand | 300 | M-2 | 35.30 | 35.37 | .77 | Muddy Sand | 25 |
| C-10 | ..... | ..... | 1.55 | Sandy Mud | 600 | M-3 | 35.34 | 35.25 | .48 | Sand | 50 |
| | | | | | | M-5 | 35.57 | 35.66 | .56 | Muddy Sand | 100 |
| D-1 | 37.10 | 35.95 | .14 | Sand | 10 | M-7 | 37.03 | 38.03 | .86 | Sand and Mud | 300 |
| D-2 | 36.92 | ..... | .31 | Sand | 25 | M-10 | 37.01 | ..... | ..... | Sand | 600 |
| D-3 | 36.40 | ..... | .47 | Sand | 50 | | | | | | |
| D-4 | 35.68 | ..... | .44 | Sand | 75 | N-1 | 35.04 | 34.92 | 1.36 | Sandy Mud | 10 |
| D-5 | 34.11 | ..... | .95 | Muddy Sand | 100 | N-2A | 36.44 | 36.89 | 1.43 | Mud-Sand Gravel | 25 |
| D-7 | 37.21 | ..... | .97 | Muddy Sand | 300 | N-2B | 34.69 | 35.70 | 1.13 | Sand | 25 |
| D-10 | 35.84 | ..... | 1.47 | Muddy Sand | 600 | N-3 | 36.94 | 37.10 | ..... | Sand | 50 |
| | | | | | | | | | | | |
| E-4 | 35.77 | ..... | .37 | Sand | 75 | O-1 | 34.42 | 34.99 | 1.48 | Mud | 10 |
| E-5 | 37.21 | ..... | .45 | Sand | 100 | O-2 | 35.03 | 36.74 | 2.16 | Mud | 25 |
| E-7 | ..... | ..... | .71 | Muddy Sand | 300 | O-3 | 35.05 | 37.00 | 1.96 | Mud | 50 |

| | | | | | |
|---|---|---|---|---|---|
| F-2 | ..... | ..... | .28 | Sand | 25 |
| F-3 | ..... | ..... | ..... | Sand | 50 |
| F-4 | ..... | ..... | .34 | Sand | 75 |
| F-5 | ..... | ..... | .29 | Sand | 100 |
| F-7 | ..... | ..... | .56 | Muddy Sand | 300 |
| G-1 | 35.44 | 36.38 | 1.00 | Muddy Sand | 10 |
| G-2 | 35.86 | 37.39 | .82 | Sandy Mud | 25 |
| G-3 | ..... | ..... | .79 | Muddy Sand | 50 |
| H-1 | 35.25 | 35.88 | .84 | Sandy Mud | 10 |
| H-3 | 36.15 | ..... | 1.49 | Sandy Mud | 50 |
| H-4 | 35.66 | ..... | ..... | Muddy Sand | 75 |
| H-5 | 35.70 | ..... | ..... | Muddy Sand | 100 |
| H-5B | 35.70 | ..... | 1.55 | Mud | 100 |
| H-7 | 35.73 | ..... | ..... | Mud | 250–300 |
| I-1 | 35.66 | 35.59 | .45 | Muddy Sand | 10 |
| I-2A | ..... | ..... | .41 | Muddy Sand | 25 |
| I-2B | ..... | ..... | .41 | Muddy Sand | 25 |
| I-2BB | ..... | ..... | .41 | Muddy Sand | 25 |
| I-2C | ..... | ..... | .41 | Sandy Gravel | 25 |
| I-3A | ..... | ..... | 1.12 | Muddy Sand | 50 |
| I-3B | ..... | ..... | 1.22 | Sandy Mud | 50 |
| I-3C | ..... | ..... | ..... | Sandy Gravel | 50 |
| I-4 | ..... | ..... | ..... | Sandy Gravel | 75 |
| I-5 | ..... | ..... | ..... | Gravelly Sand | 100 |
| I-7 | ..... | ..... | ..... | Sand | 300 |
| J-1 | 35.70 | 35.70 | .36 | Muddy Sand | 10 |
| J-2 | ..... | ..... | .94 | Muddy Sand | 25 |
| J-3 | ..... | ..... | .76 | Muddy Sand | 50 |
| O-4 | 36.62 | 35.68 | 1.89 | Sandy Mud | 75 |
| O-5 | 36.76 | 35.68 | 1.05 | Sandy Mud | 100 |
| O-7 | 35.41 | 37.66 | .76 | Sand and Mud | 300 |
| O-10 | 35.41 | ..... | .56 | Muddy Sand | 600 |
| 41 | ..... | ..... | .69 | Muddy Sand | 10 |
| 55 | 35.55 | 37.12 | ..... | Sandy Mud | 20 |
| 56 | 37.21 | ..... | 1.18 | Sand | 23 |
| 58F | ..... | ..... | .52 | Sand | 5 |
| 60C | ..... | ..... | .34 | Sand | 5 |
| 60D | ..... | ..... | ..... | Sand | 5 |
| 62A | ..... | ..... | ..... | Sand | 5 |
| 62B | ..... | ..... | ..... | Muddy Sand | 10 |
| 62C | ..... | ..... | ..... | Mud-Sand Gravel | 12 |
| 62D | ..... | ..... | ..... | Sand | 25 |
| 64 | ..... | ..... | .59 | Sandy Mud | 75 |
| 65 | ..... | ..... | ..... | Muddy Sand | 18 |
| 66I | ..... | ..... | ..... | Sand | 5 |
| 66II | ..... | ..... | ..... | Sand | 5 |
| 67A | ..... | ..... | ..... | Sand | 5 |
| 67B | ..... | ..... | ..... | Sand | 5 |
| 68 | ..... | ..... | ..... | Mud-Sand Gravel | 10 |
| 69 | ..... | ..... | ..... | Sandy Gravel | 40 |
| 70 | ..... | ..... | .90 | Sandy Mud | 5 |
| 71 | ..... | ..... | 1.31 | Sandy Mud | 25 |
| 72C | 34.60 | ..... | 1.87 | Mud | 5 |
| 74 | ..... | ..... | ..... | Sand | 25 |

*Bairdia gerda* Benson and Coleman
*Bairdia lævicula* Edwards
*Caudites nipeensis* van den Bold
*Cytherella pandora* Kornicker
*Cytherelloidea praecipua* van den Bold
*Cytherura johnsoni* Mincher
*Leptocythere* cf. *L. demisa* (Brady)
*Neocaudites* sp.
*Orionina bradyi* van den Bold
*Pellucistoma magniventra* Edwards
*Pumilocytheridea sandbergi* van den Bold
*Xestoleberis* cf. *X. expansa* Brady

Secondary Indicators

*Aurila confragossa* (Edwards)
*Kangarina bradyi* Puri
*Loxoconcha reticularis* Edwards
*Loxoconcha* sp. 1
*Orionina serrulata* (Brady)

The species of Assemblage A occur in sediment that is a mixture of mud and sand. It is not possible, on the basis of the data available, to assign the species of this assemblage to a particular range of mud-sand mixtures such as muddy sand or sandy mud. The depth range is 5 to 300 feet and the organic content is 0.35 to greater than 2.50%. The assemblage appears to be concentrated in the area between Ponce and Mayaguez, an area of relatively low physical energy. The same type of sediment occurs elsewhere around Puerto Rico. The sediments along the north coast are predominantly mud-sand mixtures. The high energy and the relatively smooth bottom topography on the north coast, however, appear to be favorable conditions for the species of Assemblage A. The geographic location of Assemblage A is shown in Fig. 2, and Plate 1 illustrates the species diagnostic of Assemblage A.

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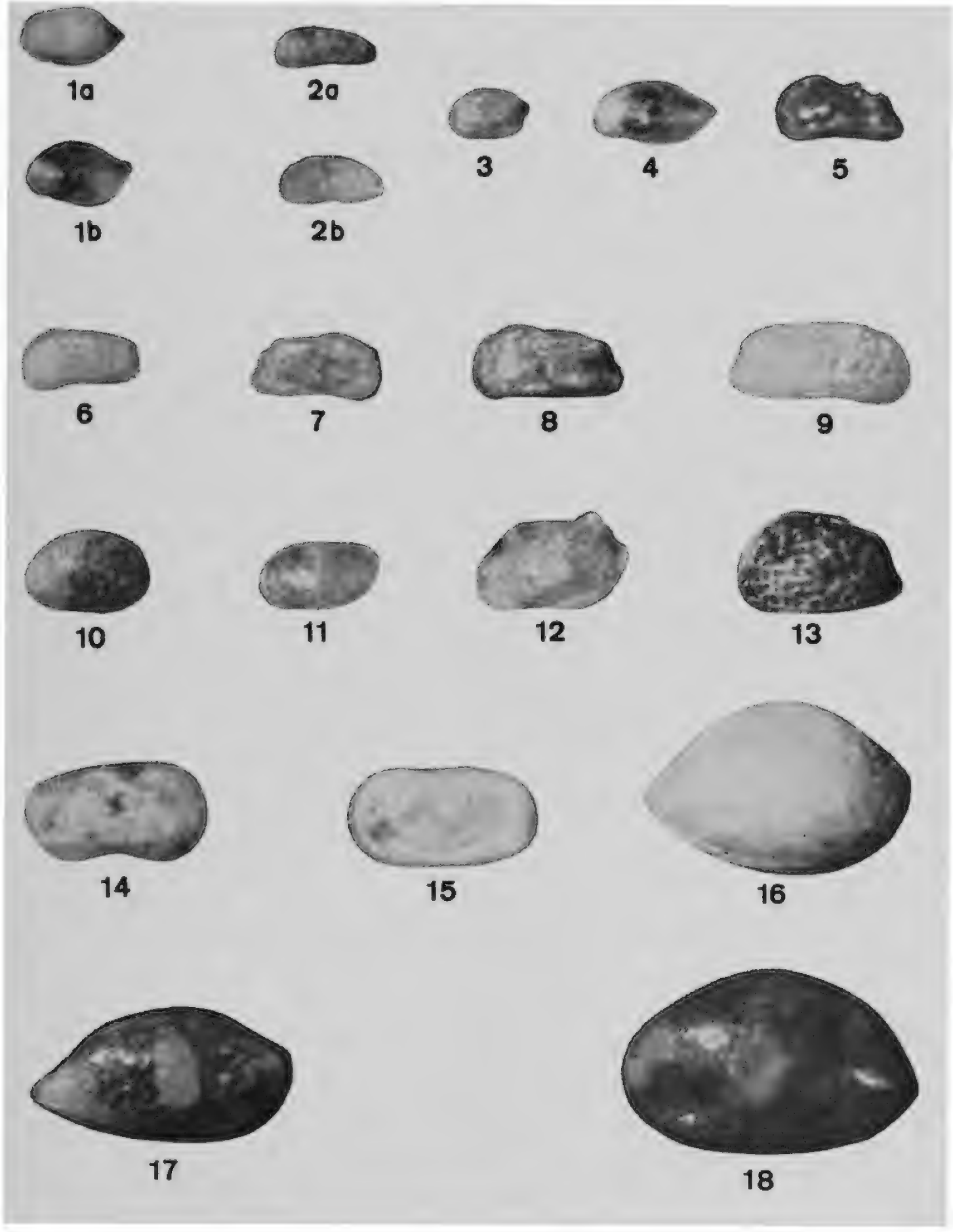
PLATE I

All figures ×40

Figure

1. a. *Cytherura johnsoni* Mincher, left valve
   b. *Cytherura johnsoni* Mincher, left valve
2. a. *Pumilocytheridea sandbergi* van den Bold, ♂, left valve
   b. *Pumilocytheridea sandbergi* van den Bold, ♀, left valve
3. *Kangarina bradyi* Puri, left valve
4. *Pellucistoma magniventra* Edwards, left valve
5. *Caudites nipeensis* van den Bold, left valve
6. *Leptocythere* cf. *L. demisa* (Brady), left valve
7. *Neocaudites* sp., right valve
8. *Orionina bradyi* van den Bold, left valve
9. *Orionina serrulata* (Brady), right valve
10. *Xestoleberis* cf. *X. expansa* Brady, left valve
11. *Loxoconcha reticularis* Edwards, left valve
12. *Loxoconcha* sp. 1, left valve
13. *Aurila confragossa* (Edwards), left valve
14. *Cytherelloidea praecipua* van den Bold, right valve
15. *Cytherella pandora* Kornicker, left valve
16. *Bairdia antillea* van den Bold, right valve
17. *Bairdia gerda* Benson and Coleman, right valve
18. *Bairdia laevicula* Edwards, left valve

Assemblage A resembles Assemblages $B_1$ and $B_2$ of Hulings and Puri (1964). Their assemblages, from the Gulf of Mexico, indicated a preference for "sand-mud mixtures." Hulings and Puri list *Cytherura johnsoni*, which also occurs in Assemblage A of this study. Also listed by Hulings and Puri are *Loxoconcha* cf. *australis*, *L. matagordensis*, and *Neocaudites nevianii*. These genera, but not species, occur in Assemblage A. Hulings and Puri (1964) state that *Pellucistoma magniventra* exhibited "no preference for sand or sand-mud mixtures." However, in Puerto Rico, *P. magniventra* appears to prefer a mud-sand mixture, with five individuals living on muddy sand.



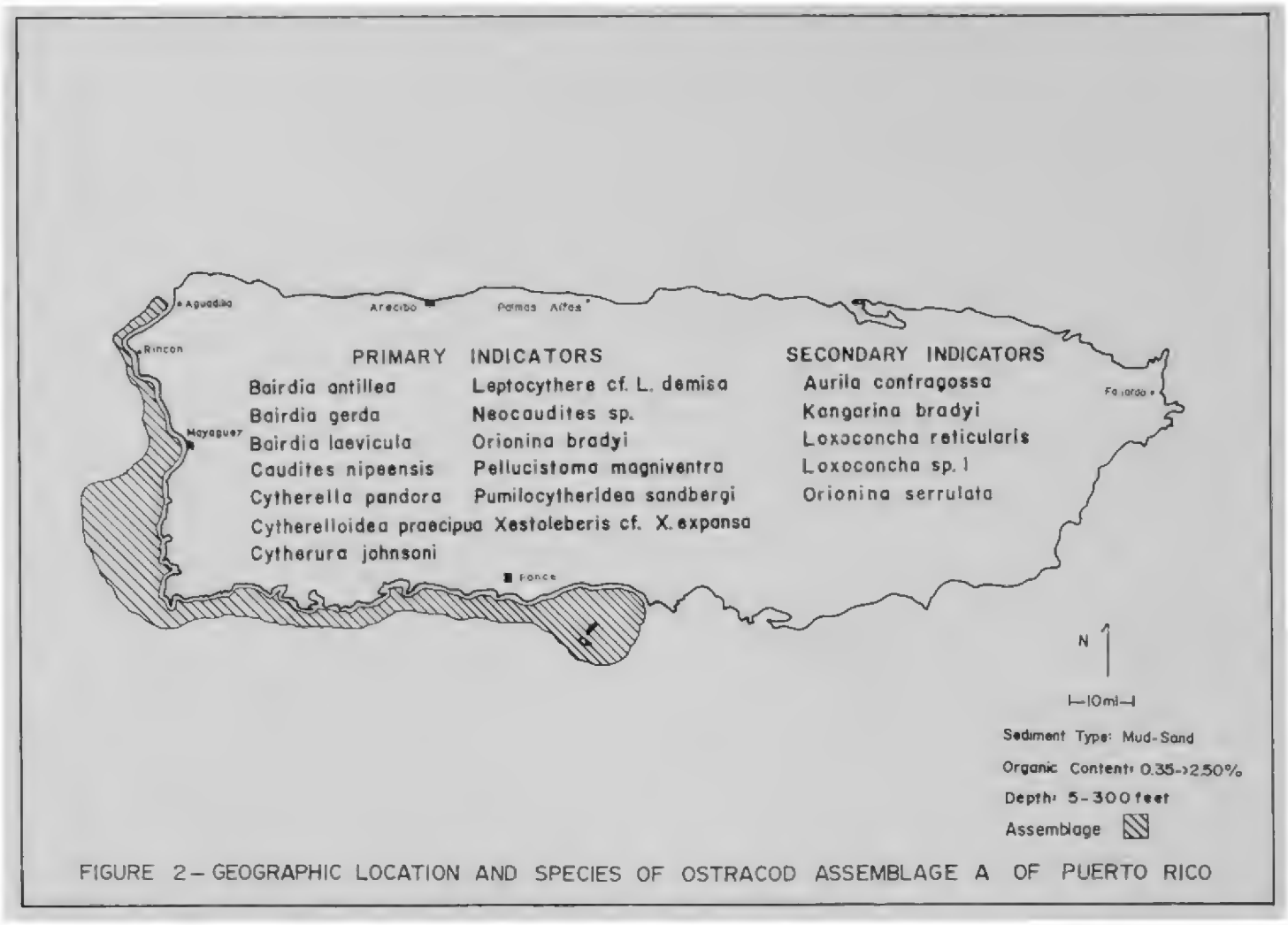



FIGURE 2—GEOGRAPHIC LOCATION AND SPECIES OF OSTRACOD ASSEMBLAGE A OF PUERTO RICO

FIG. 2. Geographic location and species of ostracod Assemblage A of Puerto Rico.

Benda and Puri (1962) found *Cytherura johnsoni* in the mangrove island assemblage of Cape Romano, Florida. The sediment of the area contained quantities of fine sand and silt, and the organic content was moderately high. Benda and Puri included *Bairdia laevicula*, *Loxoconcha reticularis*, *Neocaudites* sp. and *Pellucistoma magniventra* in the open gulf assemblage. The sediment of the open gulf assemblage consists mainly of fine, slightly shell, quartz sand. These same species also are found in Assemblage A.

Hulings (1958a) included *Cytherura johnsoni* and *Pellucistoma magniventra* in the muddy sand biozone of Apalachee Bay, Florida. These two species are included in Assemblage A. Hulings also includes *P. magniventra* in his sand biozone of the outer neritic zone off Panama City, Florida.

Key (1954) found *Caudites nipeensis*, included here in Assemblage A, in the Gulf of Paria, Trinidad. Few specimens were found at a depth of 84 feet on what Key designated as platform sands, which places this species within the depth range of Assemblage A.

Assemblage B—This assemblage includes five species as follows:

Primary Indicators

*Campolycythere striata* van den Bold
*Copytus caligula* Skogsberg
*Costa variabilcostata* van den Bold
*Cytherella grossmani* Benson and Coleman
*Neomonoceratina mediterranea* (Ruggieri)

Secondary Indicators

None

Assemblage B prefers sandy mud. The depth range is 5 to 100 feet and the organic content ranges from 0.41 to 0.95%. The geographic occurrence of Assemblage B is between Fajardo, on the east coast, and Aguadilla, on the west coast. Sandy mud also occurs on the north side of the island but the high energy, strong currents, and smooth topography of the bottom does not seem to be optimal for most of the species of this assemblage. The geographic location of Assemblage B is shown in Fig. 3. Plate II shows the species characteristic of Assemblage B.

Assemblage B does not resemble any previously reported assemblages from the Gulf of Mexico or the Caribbean. Key (1954), however, reports *Neomonoceratina mediterranea* from the Gulf of Paria, Trinidad, and states that this species was common at 120 feet. The sediment type was designated as platform sand, which resulted from being moved by currents and reworked by waves. It is not possible to correlate the sediment type of Key with that of Assemblage B.

Assemblage C—Seventeen species are included in this assemblage as follows:

Primary Indicators

*Bairdia dinochelata* Kornicker
*Bairdia* cf. *B. bradyi* van den Bold
*Bairdia* sp.
*Bythocypris laeva* Puri
*Bythocypris* sp.
*Cushmanidea elongata* (Brady)
*Cushmanidea* sp.
*Cytherella arostrata* Kornicker

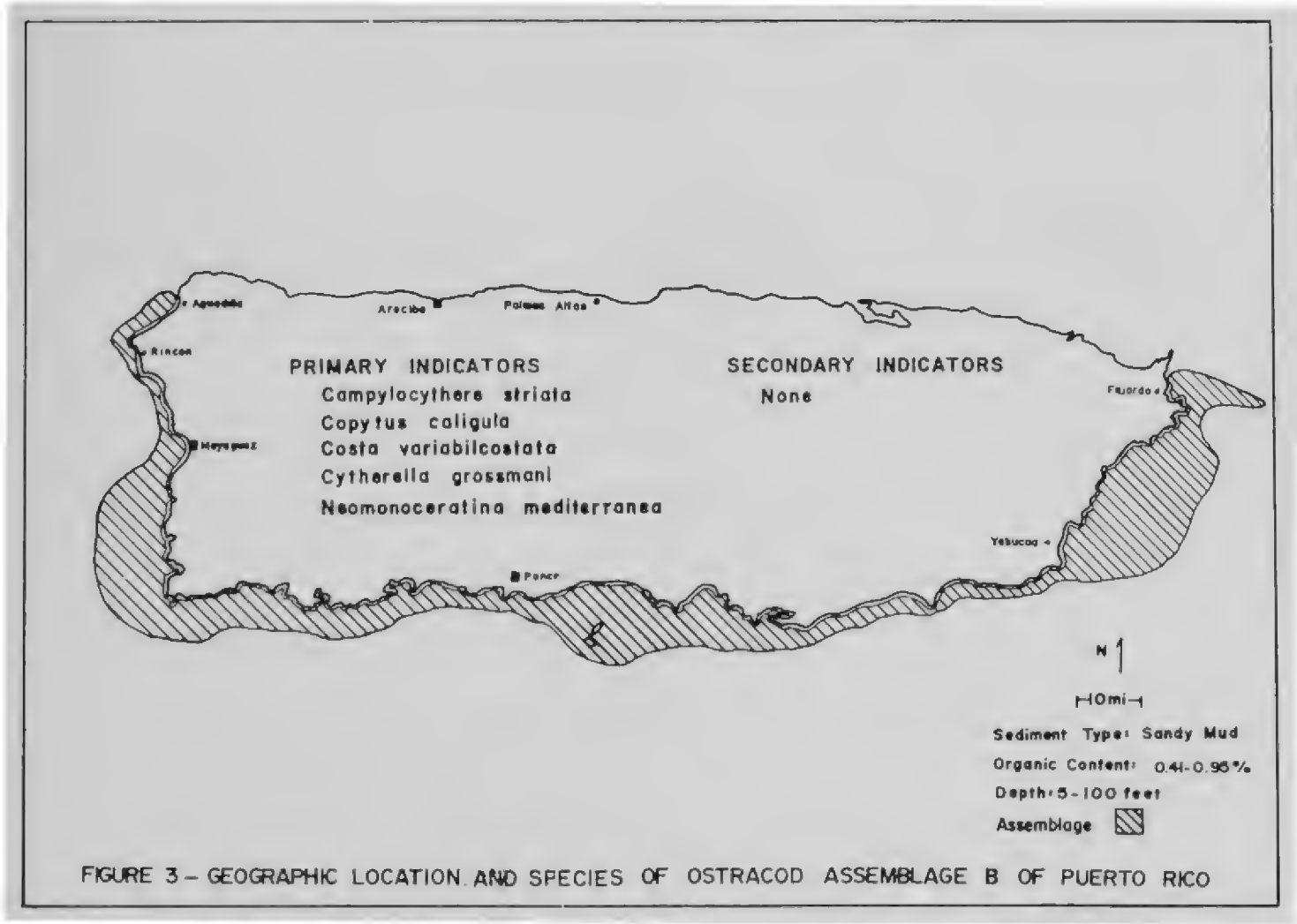



FIGURE 3 – GEOGRAPHIC LOCATION AND SPECIES OF OSTRACOD ASSEMBLAGE B OF PUERTO RICO

FIG. 3. Geographic location and species of ostracod Assemblage B of Puerto Rico.

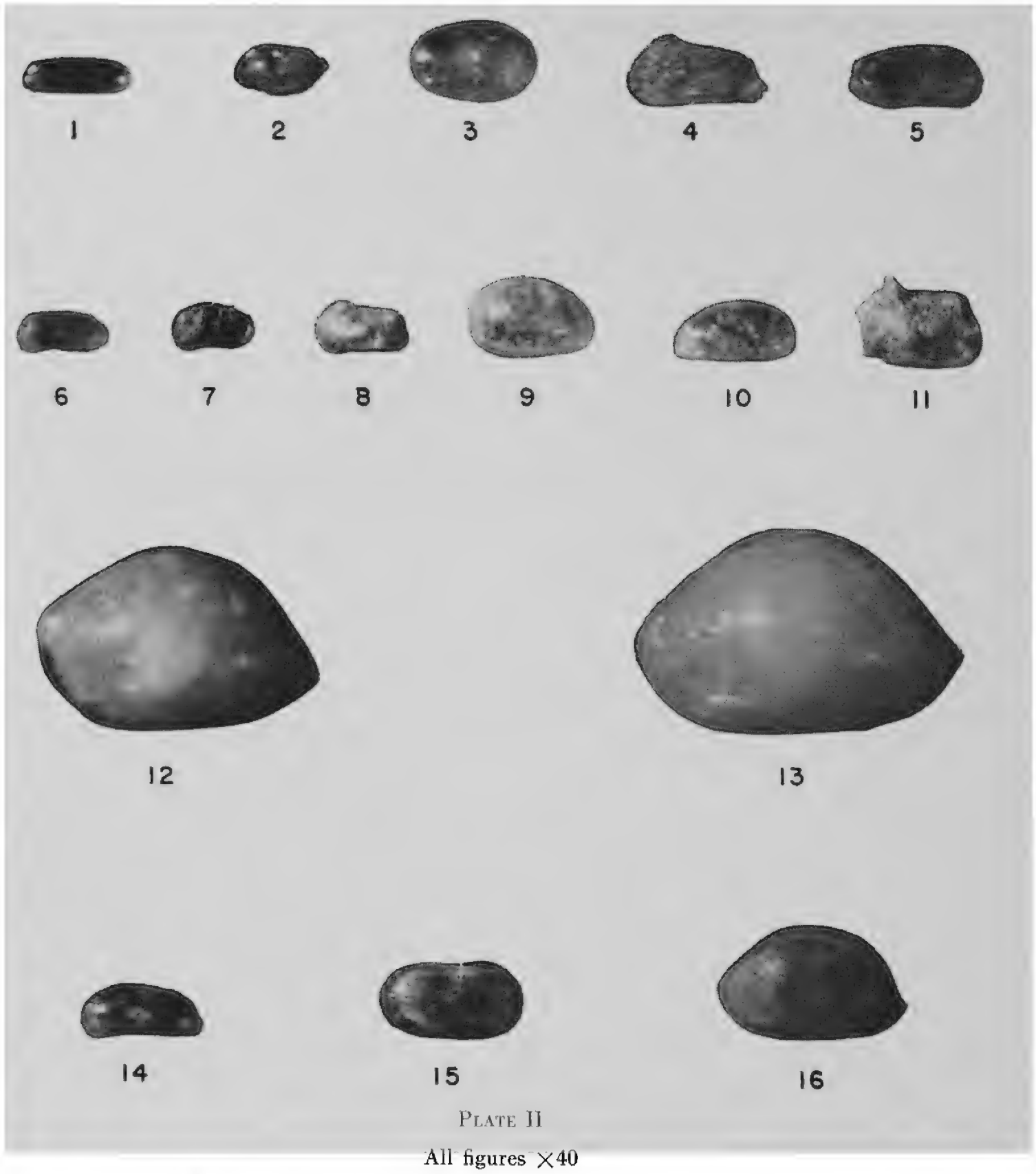



PLATE II

All figures ×40

Figure
1. *Copytus caligula* Skogsberg, left valve
2. *Neomonoceratina mediterranea* Ruggieri, left valve
3. *Cytherella grossmani* Benson and Coleman, right valve
4. *Costa variabilcostata* van den Bold, right valve
5. *Campylocythere stricta* van den Bold, right valve
6. *Microcytherura* sp., left valve
7. *Callistocythere cranekeyensis* (Puri), left valve
8. *Bradleya hornibrooki* Puri, left valve
9. *Xestoleberis margaritea* Brady, right valve
10. *Xestoleberis* sp., left valve
11. *Loxoconcha rugosa* van den Bold, right valve
12. *Bairdoppilata carinata* Kornicker, left valve
13. *Bairdia harpago* Kornicker, left valve
14. *Pontocythere* sp., left valve
15. *Cytherella* cf. *C. punctata* Brady, left valve
16. *Bairdia milne-edwardsi*, Brady, left valve

*Loxoconcha* sp. 2
*Macrocypris decora* (Brady)
*Pontocypris attenuatum* Brady
*Pontocypris* sp.
*Propontocypris* sp.

Secondary Indicators
*Loxoconcha fischeri* (Brady)
*Microcytherura fulva* (Brady and Robertson)
*Paracytheridea* cf. *P. toleri* Howe and Law
*Puriana rugipunctata* (Ulrich and Bassler)

Assemblage C occurs in mudy sand, at a depth range of 5 to 300 feet, and the organic content, in general, ranges from 0.50 to 1.50%. This group is found in the area between Ponce, on the south coast, and Palmas Altas, on the north coast. The reason that Assemblage C is not found on the east side of the island is not apparent. It possibly could be included in that area, if the sampling were not sparse. The geographic location of Assemblage C is shown in Fig. 4. Plate III illustrates the species diagnostic of this assemblage.

Assemblage C appears to resemble Hulings' (1958a, 1958b) muddy sand biozone of Apalachee Bay, Florida. Hulings lists *Cytherella*, *Pontocypris*, *Puriana*, and *Loxoconcha* as diagnostic of the muddy sand biozone. These genera occur in Assemblage C. *Puriana rugipunctata*, found in Assemblage C, was also reported by Hulings from the muddy sand biozones.

Hulings and Puri (1964) list *Bythocypris laeva* and *Puriana rugipunctata* as members

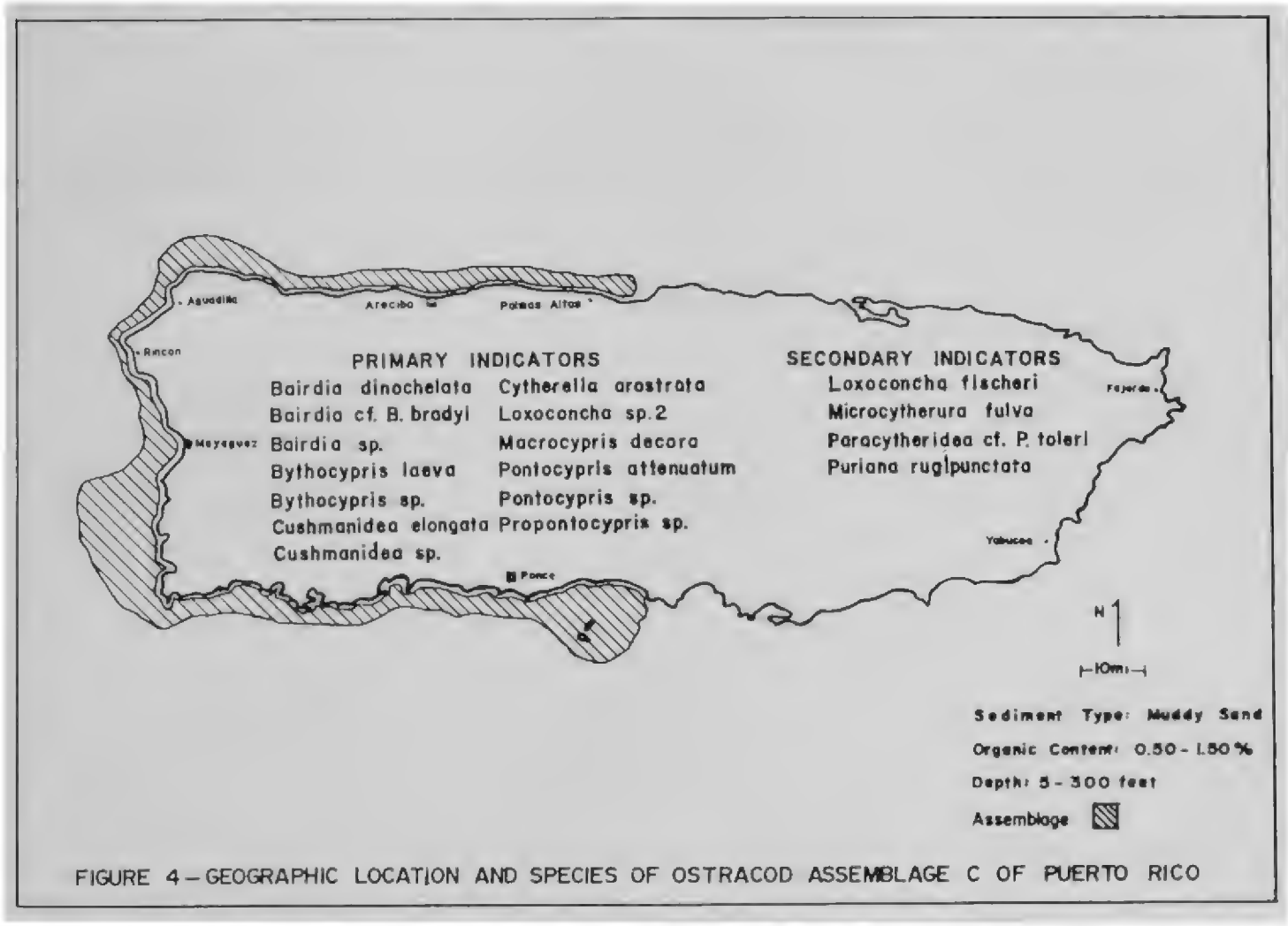
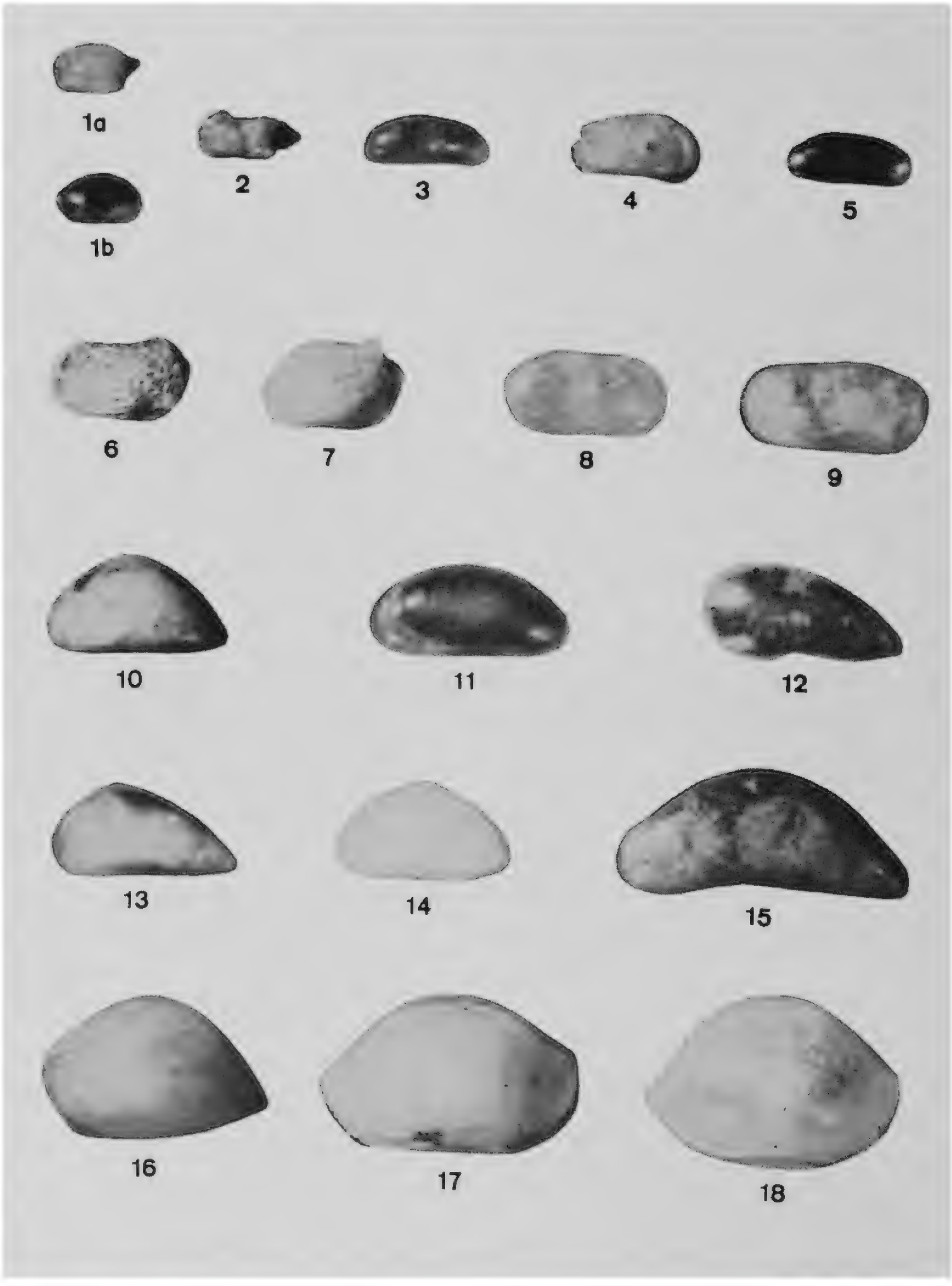



FIG. 4. Geographic location and species of ostracod Assemblage C of Puerto Rico.

of an assemblage in the Gulf of Mexico. The assemblage did not show a preference for sand and sand-mud mixtures. These two species are included in Assemblages C of this study.

Hulings and Puri (1964) list *Bythocypris laeva* and *Puriana rugipunctata* as characteristic of the open gulf assemblage. The sediment type of the open gulf consisted mainly of fine, slightly shelly sand which does not closely resemble the sediment type preferred by the species of Assemblage C.



Key (1954) found *Loxoconcha fischeri* and *Macrocypris decora* in Gulf of Paria, Trinidad. He reported two species from a water depth of 24 to 252 feet and 36 to 120 feet respectively, which places both of these species well within the depth limits of Assemblage C. *Loxoconcha fischeri* was most abundant at 24 feet from platform sands. It was common in unsorted, coarse material mixed with finest clay. *Microcypris decora*, scarce to rare in occurrence, was taken from platform sands.

Assemblage D—Three species are included in this asemblage as follows:

Primary Indicators

*Bairdia milne-edwardsi* Brady
*Cytherella* cf. *C. punctata* Brady
*Pontocythere* sp. 2

Secondary Indicators

None

The sediment type is sand, the water depth ranges from 5 to 50 feet, and the organic content is high, usually from 1.00 to greater than 2.50%. The assemblage is located in the area between Ponce and Rincon. The assemblage is restricted apparently to this area because of the lower energy and variable topography found in this region. Fig. 5 shows thte geographic location of Assemblage D, and Plate II illutrates the species characteristic of this assemblage.

The open gulf assemblage of Benda and Puri (1962) resembles Assemblage D of this investigation. Benda and Puri include *Bairdia* cf. *B. crosskeyana, B. laevicula, B. shulerae, B.* cf. *B. tuberculata,* and *Pontocythere ashermani.* These genera are included in Assemblage D. The sediment type of the open gulf assemblage corresponds closely to the sediment of Assemblage D.

Assemblage E—Eight species are included in this assemblage as follows:

Primary Indicators

*Bairdia harpago* Kornicker
*Bairdoppialta carinata* Kornicker

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PLATE III

All figures ×40

Figure

1. a. *Microcytherura fulva* (Brady and Robertson), ♂, left valve
   b. *Microcytherura fulva* (Brady and Robertson), ♀, right valve
2. *Paracytheridea* cf. *P. toleri* Howe and Law, left valve
3. *Cushmanidea elongata* (Brady), right valve
4. *Puriana rugipuncata* (Ulrich and Bassler), right valve
5. *Cushmanidea* sp., left valve
6. *Loxoconcha fischeri* (Brady), left valve
7. *Loxoconcha* sp. 2, left valve
8. *Cytherella arostrata* Kornicker, right valve
9. *Cytherella arostrata* Kornicker, left valve
10. *Bythocypris* sp., left valve
11. *Bythocypris laeva* Puri, left valve
12. *Pontocypris* sp., left valve
13. *Pontocypris attenuatum* Brady, left valve
14. *Propontocypris* sp., left valve
15. *Macrocypris decora* (Brady), left valve
16. *Bairdia dinochelata* Kornicker, left valve
17. *Bairdia* cf. *B. bradyi* van den Bold, right valve
18. *Bairdia* sp., right valve

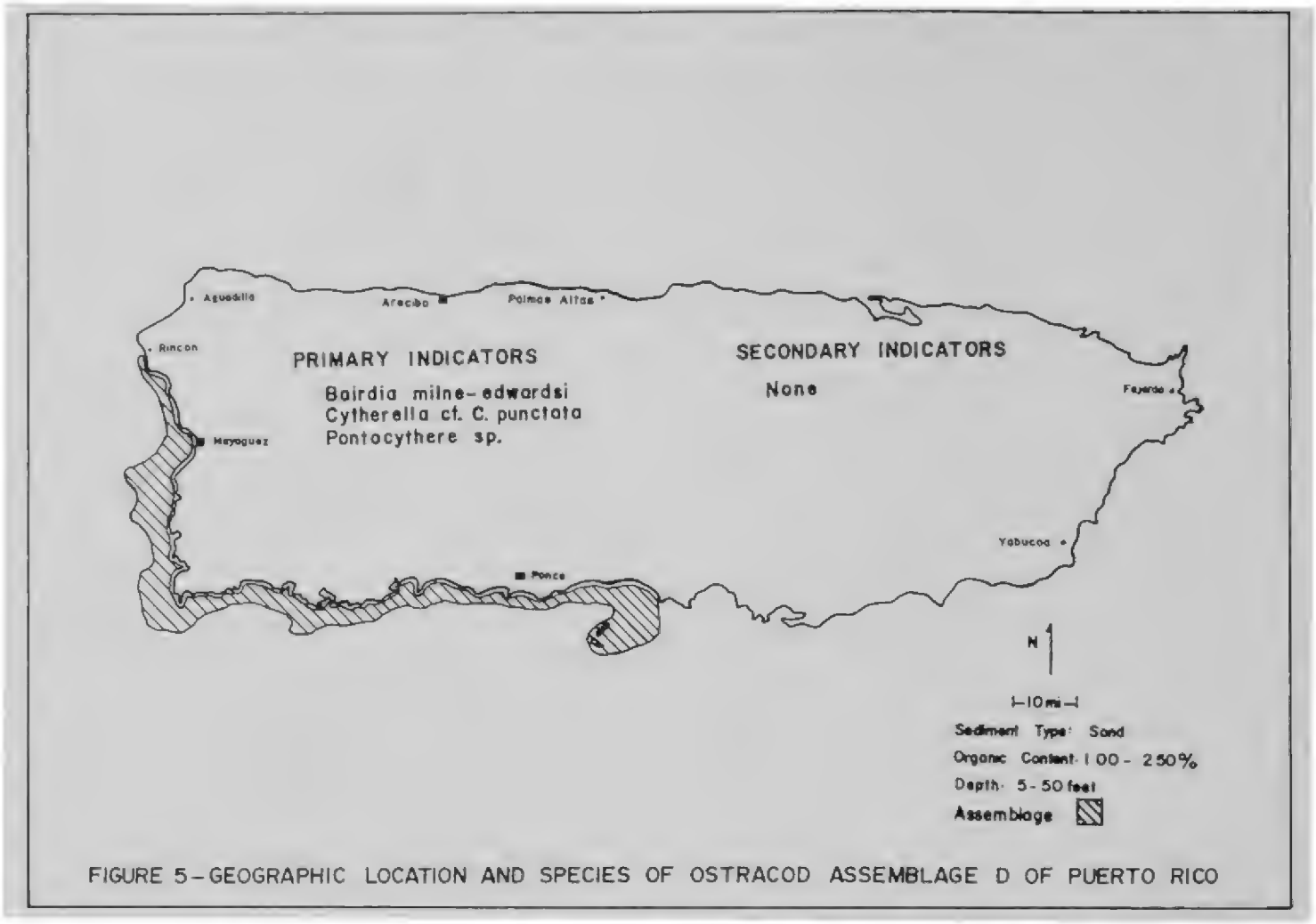


FIGURE 5 – GEOGRAPHIC LOCATION AND SPECIES OF OSTRACOD ASSEMBLAGE D OF PUERTO RICO

FIG. 5. Geographic location and species of ostracod Assemblage D of Puerto Rico.

*Microcytherura* sp. 2
*Xestoleberis margaritea* Brady
*Xestoleberis* sp.

Secondary Indicators
*Bradleya hornibrooki* Puri
*Callistocythere cranekeyensis* (Puri)
*Loxoconcha rugosa* van den Bold

These species are found at depths ranging from 5 to 600 feet, they are associated with all types of sediment, and the organic content of the sediment ranges from 1.13 to greater than 2.50%. This assemblage is located in the area between Ponce and Mayaguez. The assemblage, like Assemblages A, B, and D, occurs in an area of low physical energy, reduced currents, and rough topography. The geographic location of Assemblage E is shown in Fig. 6, and Plate II illustrates the species diagnostic of this assemblage. There does not appear to be a strict counterpart to this assemblage in the literature.

## COMPARISON WITH THE OSTRACOD FAUNA OF THE GULF OF MEXICO AND CARIBBEAN SEA

The ostracods found in this investigation represent the greatest number of species yet reported from any region in the Gulf of Mexico or Caribbean Sea. This is expected since tropical areas, in general, are characterized by a larger number of species when compared to non-tropical areas. In terms of the number of individuals per species, the number is generally lower in tropical areas than in non-tropical areas. The largest number

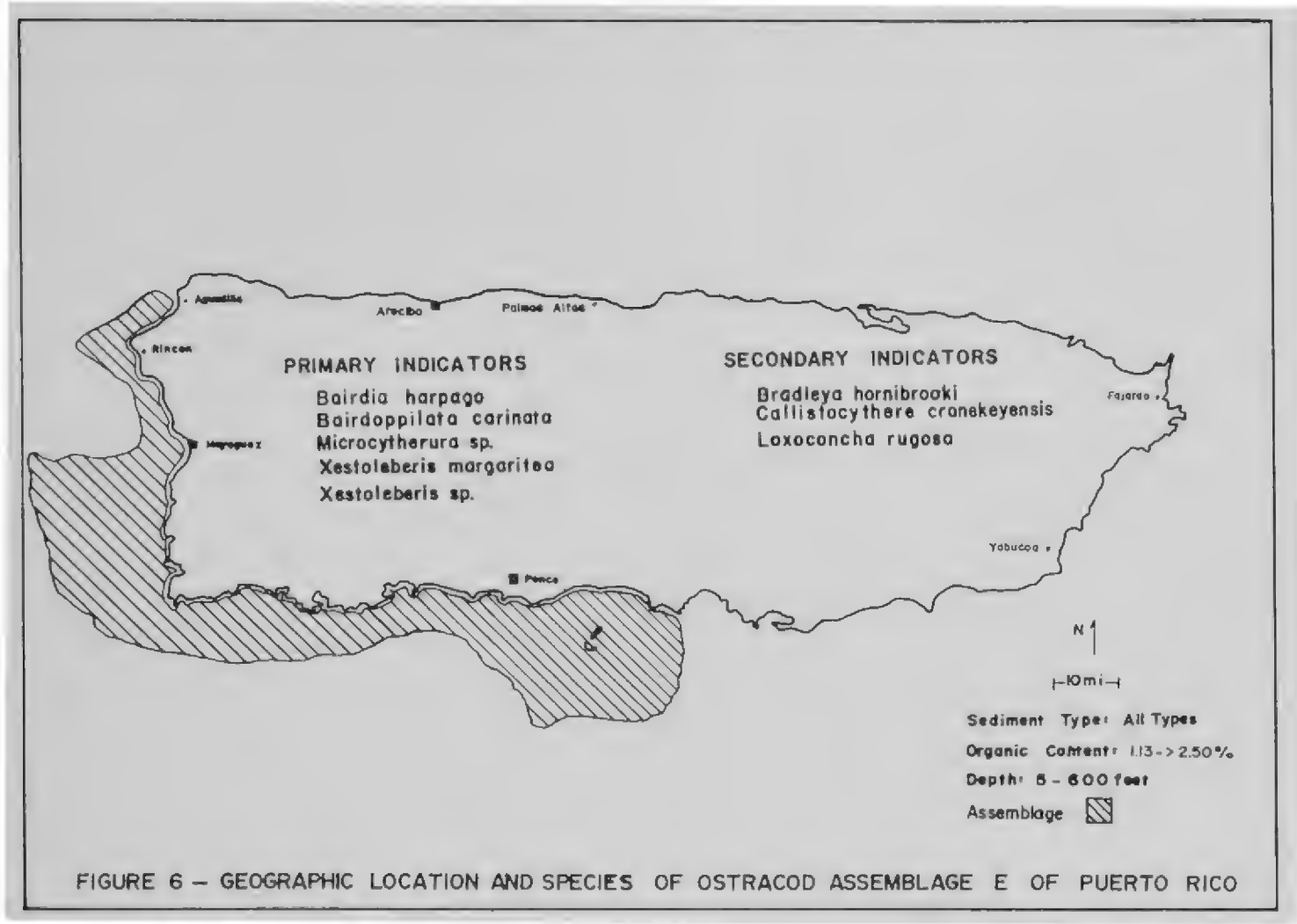


FIGURE 6 – GEOGRAPHIC LOCATION AND SPECIES OF OSTRACOD ASSEMBLAGE E OF PUERTO RICO

FIG. 6. Geographic location and species of ostracod Assemblage E of Puerto Rico.

of ostracod species previously reported from the Gulf and Caribbean occurred in areas along the west coast of Florida. This region is in part subtropical and in part tropical. The ostracod fauna of the west coast of Florida is dominated by species of the family Trachyleberididae. In this investigation, the same group is also dominant with 11 genera and 20 species. The trachyleberids found included *Bradleya hornibrooki* Puri, *Bradleya* sp., *Buntonia* sp., *Carivella navis* Coryell and Feilds, *C.* cf. *C. semitranslucens* (Crouch), *Costa variabilcostata* van den Bold, *Costa* sp., *Jugosocythereis vicksburgensis* (Howe), *Neocaudites triplistriata* (Edwards), *Neocaudites* sp., *Occultocythereis angusta* van den Bold, *Orionina bradyi* van den Bold, *O. serrulata* (Brady), *O. vaughani* (Ulrich and Bassler), *Quadracythere aequalis* van den Bold, *Q. antilles* van den Bold, *Quadracythere* sp. and *Trachyleberis* sp. The two dominant genera in the Puerto Rican fauna were *Bairdia* and *Xestoleberis*. *Bairdia* was found to be represented by 17 species, 10 named and 7 unnamed. The named species not previously mentioned include *B. tuberculata* Brady and *B.* cf. *B. expansa*. *Xestoleberis* was represented by 19 species, 8 named and 11 undetermined. The former included *X. curta* Brady, *X. depressa* Sars, *X. granulosa* Brady, *X. margaritea* Brady, *X. varigata* Brady, *X*, cf. *X. expansa* Brady, *X.* cf. *X. labiata* Brady and Robertson and *X.* cf. *X. setigera* Brady. The numbers are considerably greater than the number of species reported for both of these genera from the Gulf of Mexico. In this study, *Bairdia* occurs in four of the Assemblages A, C, D, and E. This indicates the wide diversification of this genus in Puerto Rico. There is also an indication that both groups need more detailed study.

Several of the Puerto Rican species have not heretofore been described from either the Gulf of Mexico or the Caribbean Sea. However, about 50 of the Puerto Rican species

have previously been reported from the Gulf of Mexico. Only five species from Puerto Rico were found by Key (1954) in the Gulf of Paria, Trinidad, and 29 species were found by van den Bold (1963c) in the Recent sediments of Trinidad. It appears, therefore, that the ostracod fauna of Puerto Rico has much in common in terms of species with the Gulf of Mexico and other areas in the Caribbean Sea. It is also reasonable to assume that the Recent Puerto Rican fauna is closely related to the Tertiary fauna of the Caribbean. A detailed study should support this thesis.

## Acknowledgments

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# Seasonal Occurrence of Fishes in a Coastal Marsh of Northwest Florida[1]

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## Abstract

The biota of a Northwest Florida coastal marsh was analyzed, and the relation of salinity and temperature to the fish population was studied for one year. It was concluded that variations in temperature had a greater influence upon the variation in fish populations than did salinity fluctuations.

## Introduction

Along the northwestern Gulf Coast of Florida, in the region where the peninsular portion of the state joins the northern panhandle, the intertidal marsh reaches its maximum extent in Florida. In this area, many people have sought to determine the composition of the biota and work out the life histories of some of the conspicuous fishes (Jordan, 1884; Breder, 1940; Kilby, 1948, 1950, 1955; Moody, 1950; Kurz, 1953; Caldwell, 1954, 1955; Kurz and Wagner, 1957).

Although the northern part of the extensive marsh zone is continuous with the more southerly region, no specific studies have been made in the less accessible panhandle portion. However, upon the decision of the Florida Game and Fresh-Water Fish Commission, in conjunction with a large landholder, to alter the physiography of a small portion of the northern marsh area, it was decided that a thorough study of the biota and environmental conditions was in order.

## Description of the Research Area

The area under study is 700 acres (284 hectares) of estuarine waters and marsh located about eight miles (13 km) south of U.S. route 98, halfway between Newport and Perry, Florida. The metropolitan areas of Tallahassee and Perry are located 55 miles (88 km) to the northwest and 40 miles (64 km) to the east, respectively (Fig. 1). State road 14 crosses route 98 and extends south to the Econfina River about three miles (4.8 km) southwest of the impoundment site. From the river a logging road leads to the waters of Coker Creek, where the main station for the study is based (Fig. 2).

The area, which consists of an extensive marsh, including several ponds and creeks, is under tidal influence. The northernmost reaches are affected only by spring tides and during periods of extensive flooding. The region lies between the Gulf of Mexico and higher ground occupied by stands of Sabal-palm and Long-leaf Pine. The western boundary is delineated by the Econfina River, and the eastern boundary is continuous with

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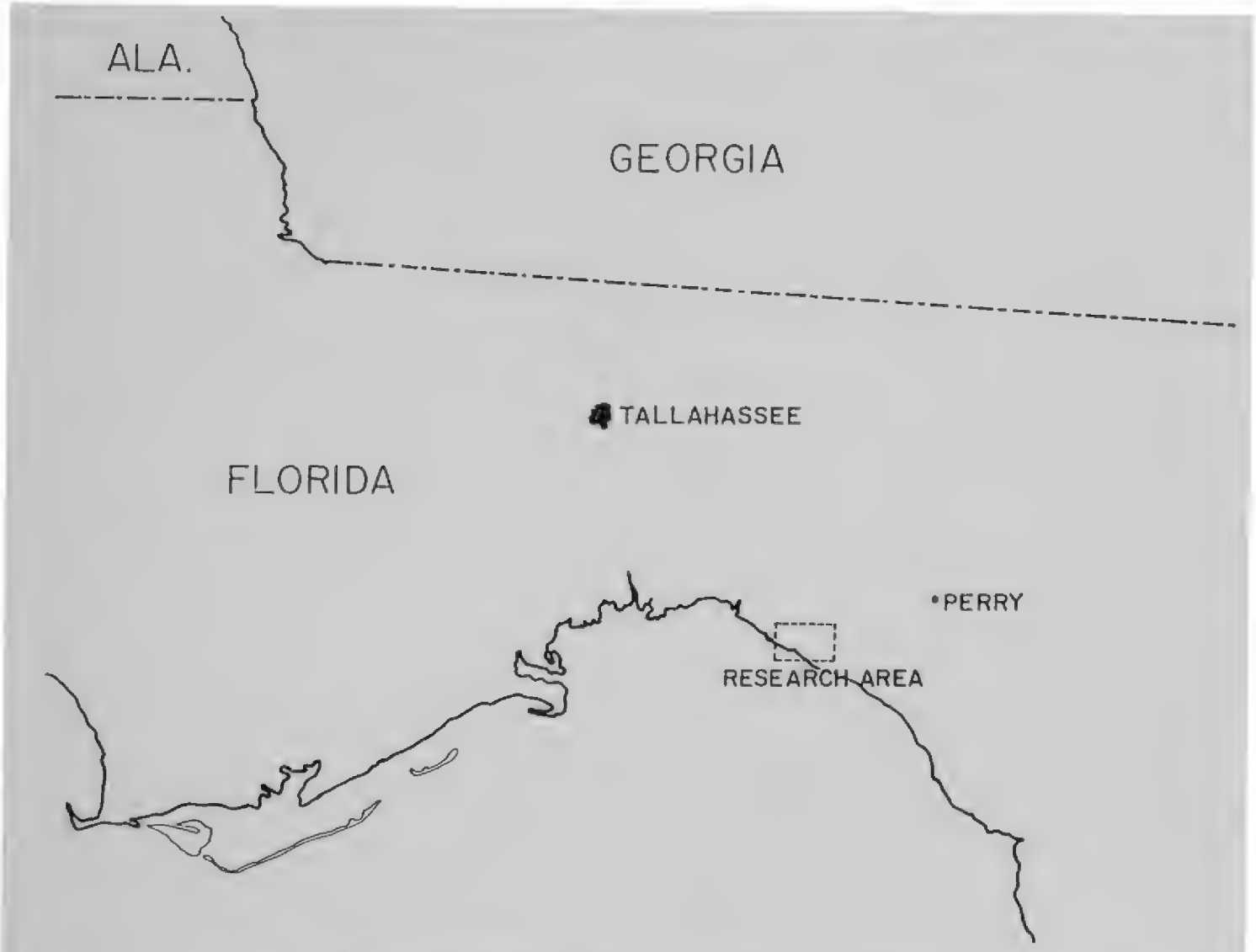


FIG. 1. Geographical location of the research area.

similar estuarine marsh (Fig. 2). Numerous hammocks with their abundant growth of trees and shrubs generally remain above water when the marsh land is flooded.

## Methods

The biological components of several types of marsh habitats were sampled with either a 30 × 5-foot or a 15 × 3¾-foot seine (⅜ inch mesh). The 15-foot seine was dragged twice along the entire shoreline of the pond, or for 91 m along the edge of the creek. The 30-foot seine was then dragged across the diameter of the pond or 46 m up the center of the creek. The sampling period extended from December 21, 1963 through January 30, 1965.

Salinity samples were collected at mid-depth, transported to the laboratory in tightly-capped jars, and determined with a G. M. Mfg. Co. hydrometer. Air and water temperatures were determined with a mercury-in-glass thermometer. Temperatures were taken at each station at 0.3 m above the water surface, at 2.5 cm below the water surface, and at the bottom, generally within one-half hour before and after twelve noon.

Preserved fish specimens were measured to the nearest mm and weighed to the nearest gram. Monthly growth rates of *Mugil cephalus* Linnaeus, *Leiostomus xanthurus* Lacépède and *Lagodon rhomboides* (Linnaeus) were determined by measuring 50 specimens of each species chosen at random from each collection.

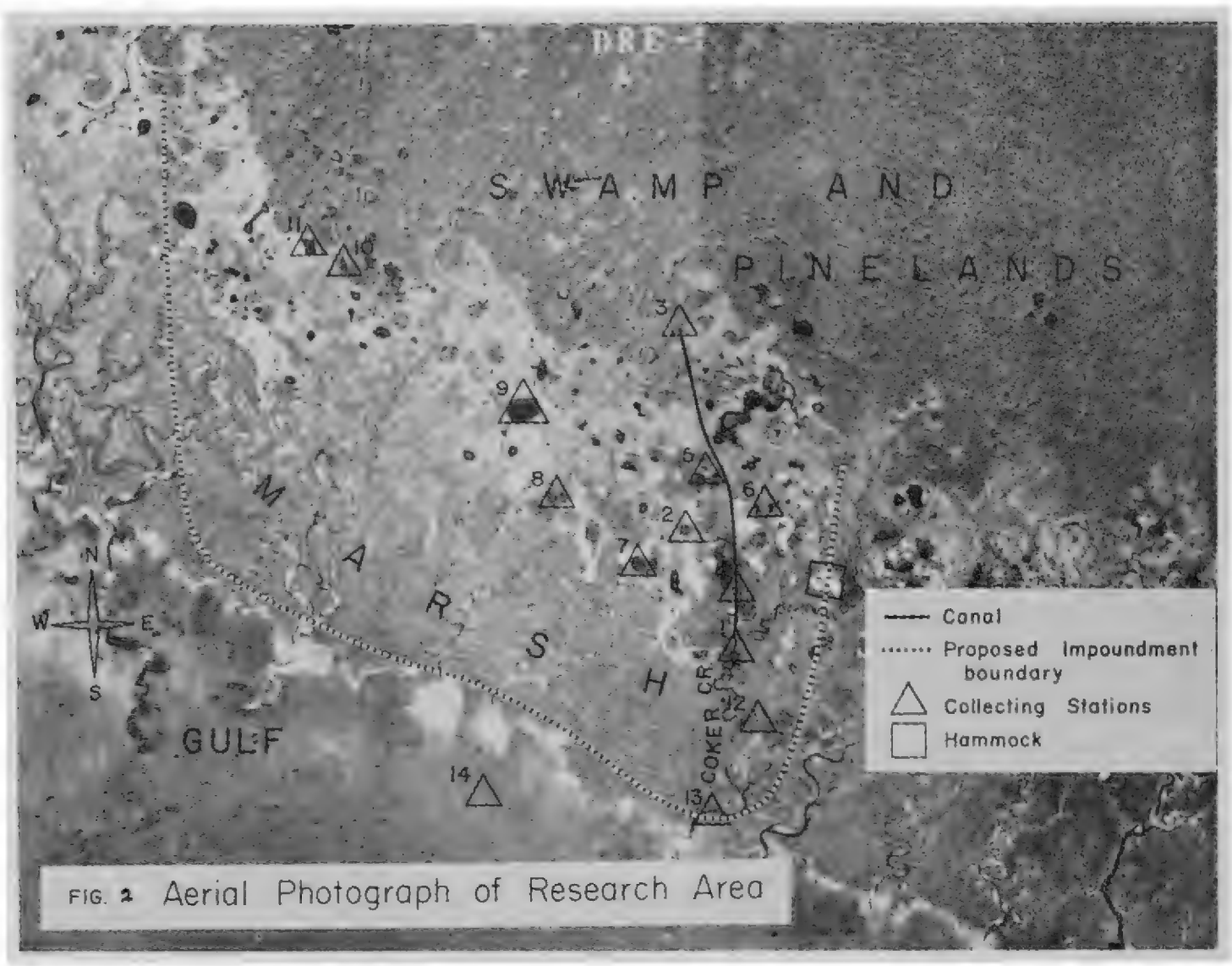


FIG. 2 Aerial Photograph of Research Area

FIG. 2. Aerial photograph of the research area, with sampling stations and landmarks as indicated.

## Results and Discussion

### HABITAT COMMUNITIES

Three distinct habitats were observed and studied. Dominant species of fishes differed among these habitats.

*Roadside Canals* (Stations 3 and 4)

The roadside canals varied from relatively deep, accessible thoroughfares, connecting ponds, to shallow, isolated stretches of water subjected to periodic desiccation. Emergent aquatic vegetation was absent, although certain areas had algae, principally *Enteromorpha flexuosa* (Wulf.), growing attached to various objects on the bottom. The bottom was either heavy organic ooze, 0.3 to 0.9 m deep, or relatively compact sandy material. A hydrogen sulfide smell was strong when the ooze was stirred.

The vegetation surrounding the canals consisted mainly of black rush, *Juncus roemerianus* Scheele, although at the canals' edges much oyster grass, *Spartina alterniflora* Loisel, was present. Several large patches of bermuda grass, *Cynodon datylon* (L) Kuntze were interspersed among the *Juncus* on higher land. The marsh elder, *Iva frutescens* L., and the sea ox-eye, *Borrichia frutescens* (L), were also conspicuous on the higher land.

Fish populations in the canals varied according to the particular part of the canal in which they were located. With the exception of the spring season, the upper portions

of the canals were dominated numerically by *Lucania parva* (Baird and Girard) and *Gambusia affinis* (Baird and Girard). The several species of *Fundulus* and *Mollienesia latipinna* LeSueur appeared to predominate in the lower regions, although *Mugil cephalus* (one year age group) and *Cyprinodon variegatus* Lacépède were locally conspicuous. Small specimens of *Callinectes sapidus* Rathbun (2.5–7.6 cm carapace width) were present the entire length of the canal, but were more abundant in the lower regions (Table 1).

During spring, either *Mugil, Leiostomus* or *Lagodon* replaced all or some of the other species in the canals.

The highest water temperature recorded (41 C) occurred in the isolated upper portion of the canal on June 20, 1964. It was at this time that a fish kill was observed.

No regular year-round collecting stations were established in the canals.

*Ponds* (stations 2, 5, 6, 7, 8, 9, 10 and 11)

The ponds consisted of two types: those that were connected to the Gulf indirectly by winding, shallow tidal creeks, which were therefore subjected to daily tidal influence; and those that were completely isolated from other water during normal tides, having connection to the outside areas only during periods of extreme high tides (spring tides) or periods of flooding (Fig. 2).

The bottom sediment of all ponds consisted of heavy, grayish-black organic ooze, rich in hydrogen sulfide, from 0.3 to 0.9 m deep. In addition, several ponds were covered with cow manure.

TABLE 1

Zonal Distribution of Fishes[a] Collected

| Species | Zones | | | Species Total |
|---|---|---|---|---|
| | Canals | Ponds | Creeks | |
| *Callinectes sapidus* | 52 | 27 | 186 | 265 |
| *Elops saurus* | .... | .... | 109 | 109 |
| *Brevoortia smithi* | .... | .... | 15 | 15 |
| *Bagre marinus* | .... | .... | 2 | 2 |
| *Galeichthys felis* | .... | .... | 155 | 155 |
| *Anguilla rostrata* | .... | 6 | .... | 6 |
| *Adinia xenica* | 34 | 42 | 11 | 87 |
| *Cyprinodon variegatus* | 88 | 265 | 64 | 317 |
| *Fundulus grandis* | 23 | 115 | 45 | 183 |
| *Fundulus similis* | 27 | 62 | 55 | 144 |
| *Lucania parva* | 154 | 180 | 106 | 440 |
| *Gambusia affinis* | 230 | 102 | 46 | 378 |
| *Mollienesia latipinna* | 211 | 361 | 119 | 691 |
| *Centropristes melanus* | .... | .... | 12 | 12 |
| *Centrarchus macropterus* | .... | .... | 27 | 27 |
| *Orthopristis chrysopterus* | .... | .... | 18 | 18 |
| *Bairdiella chrysura* | .... | .... | 32 | 32 |
| *Cynoscion nebulosus* | .... | .... | 128 | 128 |
| *Leiostomus xanthurus* | 830 | 972 | 1415 | 3217 |
| *Micropogon undulatus* | .... | .... | 5 | 5 |
| *Sciaenops ocellata* | .... | .... | 87 | 87 |
| *Laodon rhomboides* | 327 | 250 | 924 | 1501 |
| *Mugil cephalus* | 1460 | 1131 | 2270 | 5861 |
| *Menidia beryllina* | 80 | 283 | 80 | 443 |
| *Paralichthys lethostigma* | 1 | 3 | .... | 4 |
| *Trinectes maculatus* | 1 | .... | .... | 1 |
| *Symphurus plagiusa* | 1 | .... | .... | 1 |

[a] Includes *Callinectes sapidus*.

The vegetation of the ponds was similar to that of the canals, and included no emergent vegetation. The dominant types of vegetation were *Spartina alterniflora* and *Juncus roemerianus* intermixed with *Cynodon dactylon*, *Iva frutescens*, and *Borrichia frutescens*. Many ponds were situated close to hardwood hammocks. Several objects lying on the bottom of ponds, including small clumps of oyster shells, had colonies of *Enteromorpha* growing on their surfaces.

The dominant species of fishes varied from pond to pond. The numerically dominant species at Station 10, for example, was *Mollienesia latipinna*, while at Station 11, only 23 m distant, *Menidia beryllina* (Cope) was dominant. Other dominant species among the several ponds included *Fundulus similis* (Baird and Girard), *Lucania parva* and *Gambusia affinis*. During spring, *Mugil*, *Leiostomus* and, to some extent, *Lagodon* became dominant.

A permanent year-round collecting station was established at Station 2 (Fig. 2).

*Tidal Creeks* (Stations 1, 12, and 13)

The head of Coker Creek (Station 1) was selected for regular sampling as representative of tidal creek habitats.

Three main zones of tidal creeks were defined on the basis of fish populations. These were: the upstream section in the vicinity of Station 1; the mid-stream section; and the downstream section where Coker Creek flowed into the Gulf. Both the upstream and downstream faunas merged gradually into the mid-stream faunal type, but the community structures of the upper and lower zones were distinct.

The entire creek was subject to daily tidal flows. The biota of the upstream portion varied widely in accordance with tides. *Elops saurus* Linnaeus, *Sciaenops ocellata* and *Cynoscion nebulosus*, all seasonally abundant at Station 1 during high tide, were never encountered there more than 2 hours before or after flood tide. Kilby (1955) did not encounter large numbers of *Elops* in the upper reaches of the tidal creeks at Bayport and Cedar Key. He did, however, collect 19 small specimens (31–153 mm) from marsh pools at Cedar Key.

The widest range of salinity, from 2 ppt on February 23, 1964, to 32 ppt on June 27, 1964, occurred at Station 1. The lowest water surface temperature recorded (11.5 C) also occurred here at noon on February 1, 1964.

The bottom sediments in Coker Creek varied from hard packed sand to heavy organic ooze. Water depth at mean sea level was 0.3 to 0.9 m. The greatest depth recorded (1.8 m at mean high tide) was located in the mid-creek zone of Coker Creek. The depth of the creek at mean high tide varied from 0.3 to 1.2 m.

The dominant vegetation also varied from upstream to downstream. At the headwaters of the creek, about 0.8 km from the Gulf, *Juncus* was the dominant vegetation, although *Spartina* was conspicuous. Kilby (1955) and Reid (1954) found similar vegetation at Cedar Key. *Spartina* was also very conspicuous on the oyster bars which rise above the shallow flats.

Turtle grass (*Thalassia testudinum* Koenig and Sims) and the manatee grasses (*Cymnodocea manatorum* Aschers and *Halodule wrightii* Aschers) were the dominant spermatophytes growing on the shallow flats at the mouth of the creek. Small patches of widgeon grass (*Ruppia martina* L.) were also noted.

Fish collections were made along the entire length of the creek. However, Station 1 at

the head of the creek was the major collecting site, where regular samples were collected and measured, and the growth rates of *Mugil cephalus*, *Leiostomus xanthruus* and *Lagodon rhomboides* were determined.

## Environmental Factors

### *Salinity*

The salinity levels at Station 1 ranged from 2 ppt in February, 1964 to 32 ppt in June, 1964 (Fig. 3). The greatest range within one month was 18 ppt (26 to 8) in July, 1964. In general the salinities were lower during the winter than during the summer. Since rainfall was not higher during winter than the summer of 1964, increased evaporation in the shallow marshes during the summer and lower tides during the winter may have accounted for seasonal salinity differences.

### *Temperature.*

Temperature fluctuated widely seasonally and day to day. The range of surface water temperature was 20.5 C (Fig. 3). The range was similar at Station 2. In shallower areas, water temperature may reach 41 C at noon. A fish kill which occurred on June 20, 1964, was attributed to this very high daytime water temperature. By darkness, however, the water had cooled to 31 C and the surviving fishes were no longer exhibiting stress.

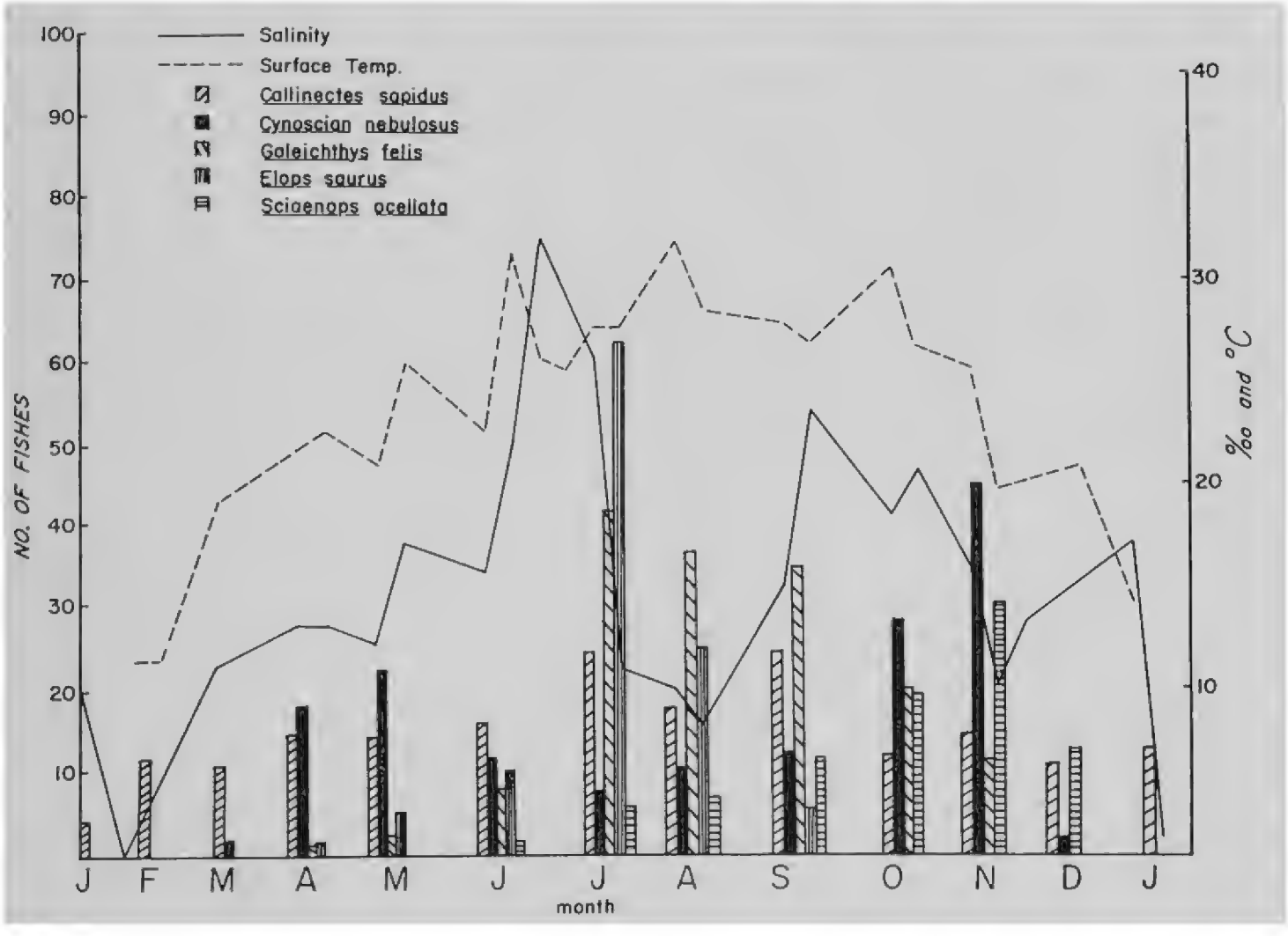


FIG. 3. Salinity, surface temperature and the abundance of the five main species of fishes at Station 1.

## Relationship of Fauna and Environment

Populations of five predator and predator-scavenger species of the fauna at Station 1 are related to both salinity and temperature (Fig. 3). No direct correlation is obvious between the abundance of the five species and salinity. Most of the species of the area are considered to be euryhaline, and some are characteristic of fresh water (Herald and Strickland, 1949).

Obviously, the fauna inhabiting the shallow estuary must be either eurythermic or must exhibit an inshore-offshore migration pattern with the varying temperatures. The resident species (Table 1) are indeed eurythermic (Parr, 1933; Pearson, 1929; Reid, 1954; Kilby, 1955).

*Callinectes sapidus* appeared to be eurythermic and euryhaline. The population level of this species remained relatively constant throughout the year. *Elops* and *Galeichthys* reached a peak during the months of highest temperatures and salinities, and were absent from December to April (*Elops* was not collected after September). *Cynoscion* seemed to prefer the cooler waters of the spring and fall months. *Sciænops* appeared in the area only after salinity had increased to the summer high. Both species attained their maximum abundance during the late fall (October and November) when both temperature and salinity were at moderate levels (Fig. 3).

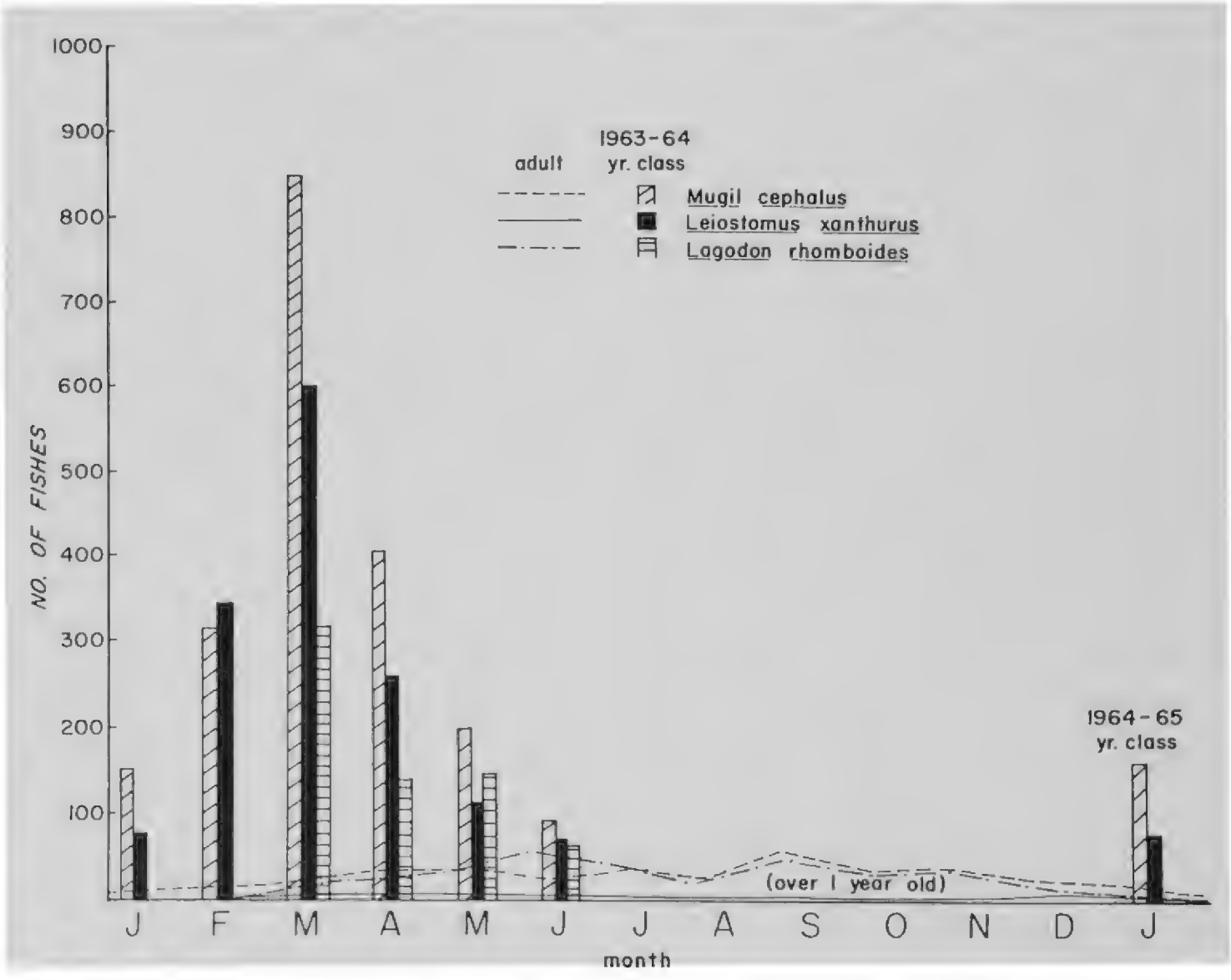


Fig. 4. Seasonal abundance of adult and juvenile *Leiostomus xanthurus*, *Mugil cephalus* and *Lagodon rhomboides* at Station 1.

During late summer and early fall (July to September) numbers and diversity of adult fishes reached a peak. The populations of three species of fishes, *Mugil cephalus*, *Leiostomus xanthurus* and *Lagodon rhomboides*, are plotted in Fig. 4. Although the adults of these species never became as abundant in the marshes as the juveniles, an increase in their populations was noted during the warmer months.

The young of *Mugil cephalus* and *Leiostomus xanthurus* appeared in collections in January, 1964. Although Gunter (1945) in Texas, and Kilby (1955) and Reid (1954) at Cedar Key have reported *Lagodon* in January, it did not appear in my samples until March. Townsend (1956) collected no juvenile *Leiostomus* during January from Alligator Harbor, Florida.

The June departure from the marsh areas for the juveniles of the three species appeared to be uniform in all of the marsh areas studied (Gunter, 1945; Kilby, 1948, 1950, 1955; Reid, 1954; Townsend, 1956). Temperature appeared to be one of the factors responsible for the exodus from the marshes.

Some of the more tropical species (such as the carangids, *Calamus, Hæmulon, Lutjanus* spp., and *Synodus*) which were reported by Reid (1954) as fairly abundant on the inshore flats at Cedar Key, were not a conspicuous part of the fauna on the flats near Coker Creek. Reid (1954) and Kilby (1955) suggested that Cedar Key may be a dividing line between the more temperate and the tropical faunas of the Florida Gulf Coast. The results of this study appear to substantiate their assumption.

The important predator species of the tidal creeks and coastal flats were essentially the same at Cedar Key and Coker Creek. These included the cobia and Spanish mackerel on the flats and trout and redfish on the flats and in the creeks. Large numbers of bluefish were found on the inshore flats at Coker Creek during the spring and early summer, although Reid (1954) stated that they were only occasionally reported inshore at Cedar Key. Reid also mentioned sharks (including large specimens) as being prominent predators at Cedar Key. In approximately 25 trips to Coker Creek, only one small shark was noted.

Growth studies of the three main species indicated a fairly rapid growth rate (Fig. 5). *Mugil cephalus* grew from an average standard length of 24 mm in January to 90 mm by June, a rate of approximately 13 mm per month. *Leoistomus xanthurus* grew 58 mm (20 to 78) from February to June and *Lagodon rhomboides* grew 34 mm (18 to 52) from March to June. In all cases the growth rate increased during the warmer months. Townsend (1956) showed a similar growth rate for the spot in Alligator Harbor, Florida.

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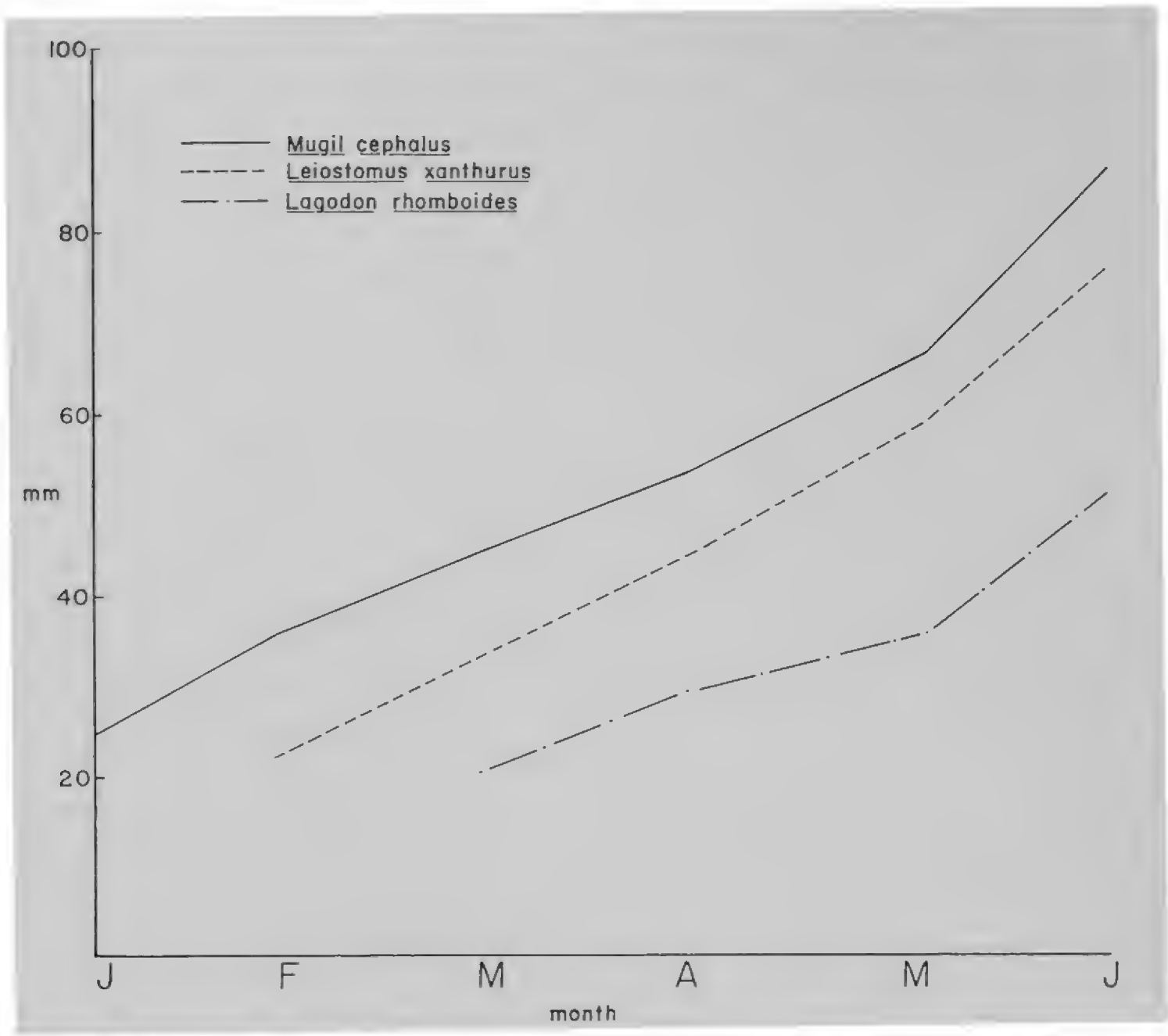


FIG. 5. Mean standard length of juvenile *Leiostomus xanthurus*, *Mugil cephalus* and *Lagodon rhomboides* at Station 1, January through June 1964.

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# Sedimentary Structures of Beach and Dune Deposits: Mustang Island, Texas

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## Abstract

Sedimentary structures of beach and dune deposits of a modern barrier island were studied in a series of trenches along Mustang Island, Texas. The following zones are characterized by distinctive stratification: 1) the foreshore by smooth, even low angle, planar cross-strata dipping gently (2 to 7 degrees) seaward; 2) the backshore by irregular strata, burrows, and locally steeply dipping (9 to 16 degrees) trough cross-strata; 3) the wind-shadow dunes by long (1 to 4 m), smooth, even, convexo-concave cross-strata; and 4) the foredune ridge by large scale, smooth, even, trough cross-strata.

The sedimentary structures observed are produced chiefly by: 1) the agent of deposition, its competence and variability; 2) the shapes and configurations of depositional and erosional surfaces; and 3) the intensity of biologic activity. The beach and dune environments are dominated by physical forces, so primary stratification predominates over biologically and chemically produced secondary structures.

The vertical succession of sedimentary structures as shown in the trenches across the beach and foredune ridge suggest an offlap sequence such as would result from prograding of the shoreline. However, the succession observed may also be the result of normal sequential development of a beach following a high storm or hurricane tide.

## Introduction

The interpretation of the depositional environments of sedimentary rocks is one of the major objectives of many stratigraphic and sedimentologic studies. Faunal and floral assemblages, textural variations, mineral composition, and sedimentary structures have all been used as environmental indicators. In many instances, especially in unfossiliferous rocks, sedimentary structures constitute perhaps the best evidence available for reconstruction of conditions at the site of deposition. The purpose of this study is to describe, differentiate, and relate the sequence of sedimentary structures in the beach and dunes of a modern barrier island to their environments of deposition and processes of formation. It is hoped that the data presented here will contribute to the understanding and interpretation of ancient sedimentary rocks deposited in similar environments.

The field studies were made on Mustang Island, Texas (Fig. 1). At each of seven stations 4 or 5 L-shaped trenches 2 to 4 m long and approximately 1 m wide were oriented so as to expose sections both parallel and perpendicular to the trend of the beach. The depths of the trenches were limited by the water table which was encountered from less than 0.5 to more than 1.5 m below the surface. The walls of the trenches were allowed to dry, lightly brushed, and photographed. The thickness, apparent magnitude and direction of dip of the stratification was then measured on these walls.

According to Thornthwaite's (1948) climatic classification the area is located in a

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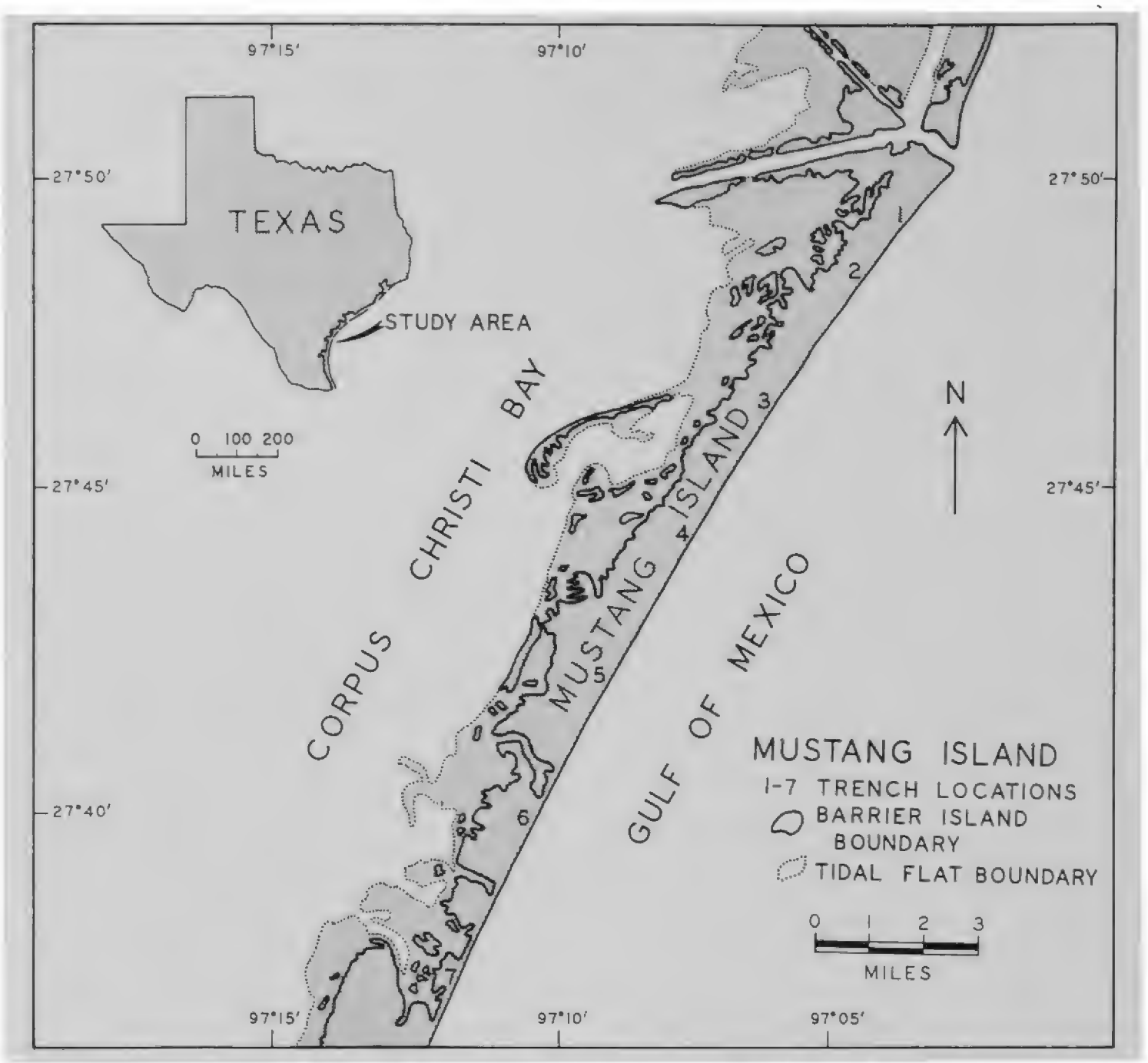


FIG. 1. Index map showing location of stations along Mustang Island.

gradational zone between the semi-arid climate of extreme south Texas and the dry, sub-humid climate of south-central Texas. Southeasterly (onshore) winds predominate most of the year, but occasional strong northerly winds accompany southward moving cold fronts (northers) in the winter months. Lunar tides range between daily and semi-daily and are generally less than 1 m. Waves along the Gulf beach are usually 0.5 to 1 m in height. However, during hurricanes and storms tides may reach 5 m above mean sea level and waves may be 3 to 5 m high.

Tourism is the major industry of the island, and human activities which may effect beach structures include regular automobile traffic on both the foreshore and backshore and camping and picnicking chiefly on the backshore.

## GEOMORPHOLOGICAL ZONATION

Mustang Island can be subdivided morphologically into five major zones (Fig. 2). From the Gulf landward they are: 1) shoreface (submerged seaward portion of the

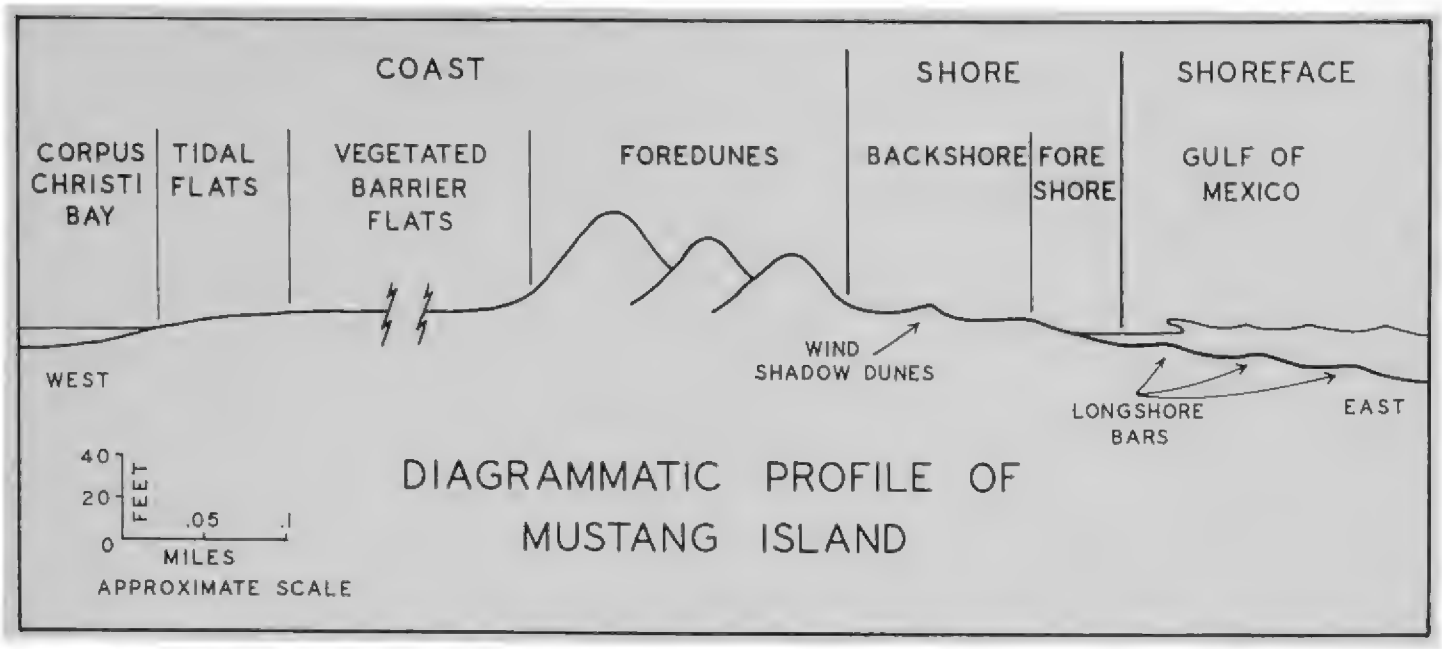


FIG. 2. Diagrammatic profile perpendicular to trend of Mustang Island showing the major topographic sub-divisions.

barrier); 2) beach (foreshore and backshore); 3) foredune ridge; 4) barrier flat (sometimes dune covered); and 5) tidal flat. The sedimentary structures were studied in detail in zones 2 and 3.

The foreshore, as defined by Johnson (1919), is that portion of the shore over which the waterline migrates as the tide changes. However, because the tide range changes daily, weekly, monthly, and seasonally, the defined limits are rather ephemeral. The zone is characterized by a width of 25 to 50 m and a smooth, regular surface sloping 3 to 6 degrees seaward. The lower and upper limits of this surface correspond closely to, and thus should perhaps be defined by, mean low water and mean high water respectively. The inner margin of the foreshore, the beach face, lies 0.5 to 1 m above mean sea level and is marked by a slight decrease in slope referred to as the berm. This is sometimes accentuated by a line of shells and other debris deposited at the crest during high tide, but at other times the beach face merges imperceptibly with the backshore without apparent discontinuity. In many instances former berm crests are denoted by sand ridges of low relief (less than 20 cm) paralleling the beach. Beach cusps sometimes develop on the foreshore; their flanks form a series of surfaces sloping (0.5 to 3 degrees) subparallel to the trend of the shore. The cusps are usually spaced 15 to 20 m apart.

The backshore extends from the berm crest landward to the seaward base of the foredune ridge and ranges from 50 to 200 m in width. The backshore is characterized by a relatively flat, horizontal to slightly sloping (landward or seaward) surface which is 1 to 2 m above mean sea level. This zone is inundated only by high spring tides or those accompanying storms or hurricanes. The surface is not so smooth and regular as that of the foreshore. Whereas the foreshore is usually damp, the backshore is usually dry. Sand can commonly be seen being carried across the backshore landward by the predominating southeasterly onshore winds. Northers carry sand in the opposite direction during the winter, but net movement is landward leading to the formation of the foredune ridges.

In several localities small dunes have formed on the backshore in the lee of patches of vegetation. These wind-shadow dunes are tear shaped in outline ranging in length

from less than 1 to more than 6 m, in width from less than 0.5 to more than 2 m, and in height from less than 0.5 to more than 1 m. The blunt end of the dune faces seaward and has a triangular shaped tail of sand extending landward. The trends of the tails of the dunes range in azimuth from 300 to 320 degrees indicating a net transport of sand in this direction. Slip faces have developed on the tails at oblique angles (southwest and northeast) to the wind direction. The crests of the tails slope landward from 2 to 10 degrees; slopes on the slip faces range from 20 to 30 degrees.

The foredune ridge complex ranges in width from 75 to more than 300 m. There are two foredune ridges which parallel the beach. In many places a third, small (1 to 2 m above the berm) ridge has been formed by the landward migration and coalescence of wind-shadow dunes. Landward of this the primary ridge is stabilized by vegetation, well defined, and extends the length of the island reaching elevations of 5 to 8 m. The other ridge which appears from its most landward position to be oldest, is confined to the northern end of the island. These dunes are heavily vegetated and reach elevations of 8 to 12 m.

The sands comprising Mustang Island are fine to very-fine and well sorted but are not very well rounded. Mineralogically, the sands are predominantly composed of quartz with secondary amounts of feldspar, chert, and opaque minerals, and according to Folk (1954) would be classified as a texturally mature subarkose.

## Sedimentary Structures

Due to the high degree of sorting, monomineralic character, and small percentage of dark, heavy minerals, the deposits forming Mustang Island lack conspicuous stratification. The observed stratification results for the most part from slight differences in textural properties of individual strata.

### Foreshore

The stratification of the foreshore is similar to that reported by other authors (Thompson, 1937; McKee, 1957; van Straaten, 1959; Bernard, LeBlanc, and Major, 1962; Soliman, 1964). It is characterized by smooth, even, low angle, planar cross-strata dipping gently seaward. The apparent dips observed in the trench walls oriented normal to the shoreline range from 2 degrees landward to 7 degrees seaward, the average is 4 degrees seaward. Dips of similar amounts at oblique angles to the beach result from regularly spaced beach cusps. High angle (20 to 30 degrees) landward dipping cross-strata like those described from the foreshore of Sapelo Island, Georgia (Hoyt, 1962) were not observed.

The cross-strata are thinly laminated to very thinly bedded (classification of McKee and Weir, 1953) ranging in thickness from 3 to less than 0.05 cm. Generally they can be grouped into several sets separated by erosion surfaces. In most cases the sets of seaward dipping cross-strata are truncated by the less steeply dipping (1 to 2 degrees) erosional surfaces. The sets thicken or thin seaward giving them a wedge-shaped appearance (Fig. 3).

In the lower portions of several trenches fine shell cross-strata dip 2 to 4 degrees seaward. These were easily recognized for they coincide with planes of weakness along

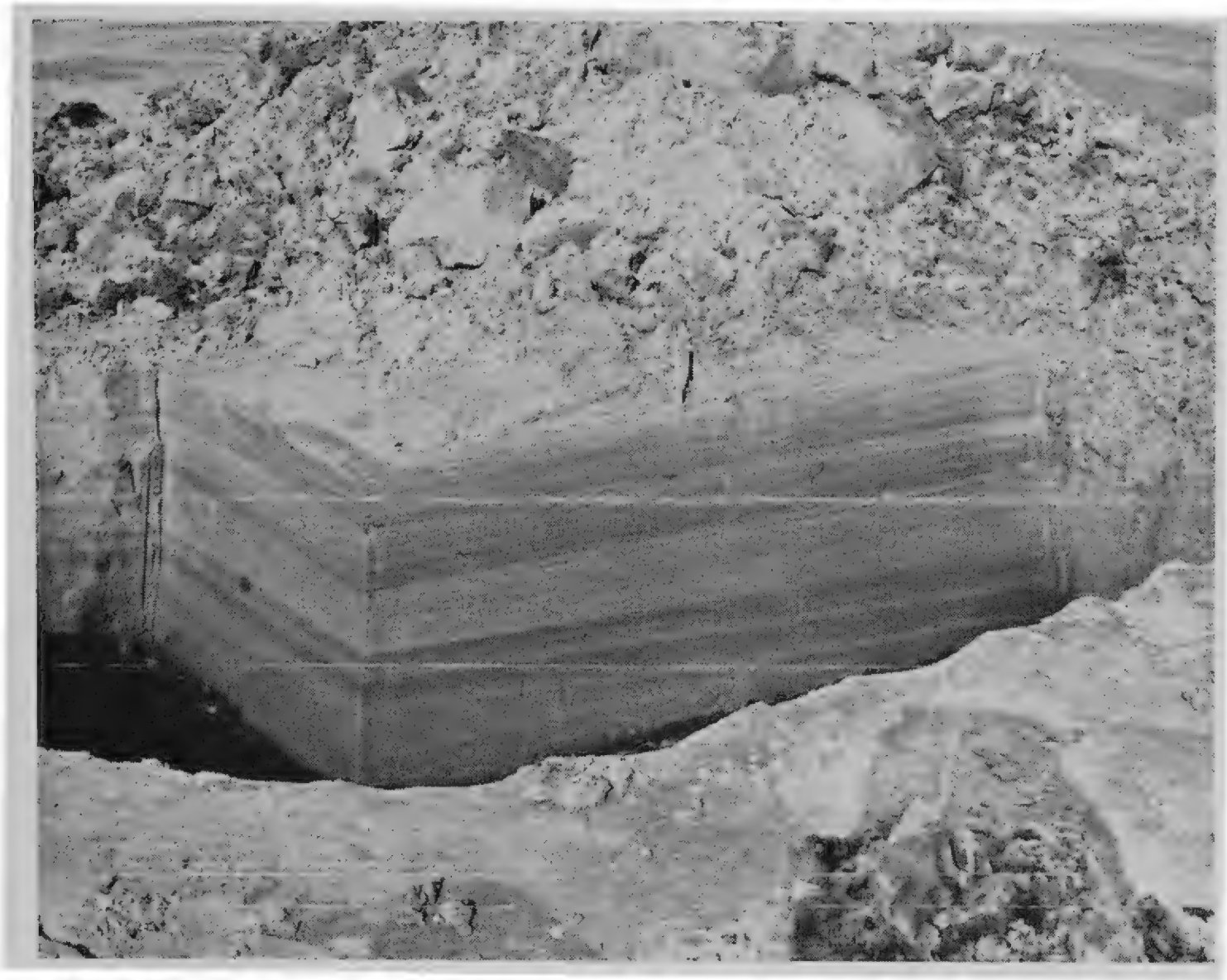

FIG. 3. Trench in lower foreshore at Station 1 showing a wedge-shaped set of low angle cross-strata dipping (2 to 4 degrees) and thickening seaward (to the right). Pencil lies above face perpendicular to beach.

which parting surfaces develop (Fig. 4). These layers resemble the very fine shell hash which covers that portion of the beach which is exposed only during maximum low tides (the uppermost shoreface). The superposition of foreshore deposits over shoreface deposits in many of these trenches suggests a prograding shoreline.

## BACKSHORE

The stratification of the backshore deposits is characterized by irregularities and locally steeply dipping cross-strata. Apparent dips range from 9 degrees landward to 16 degrees seaward. The cross-strata range in thickness from 2 to less than 0.1 cm and on the average appear to be thicker than those of the foreshore. Sets range in thickness from 3 to 36 cm and also appear to be thicker than those of the foreshore. The sets can be distinguished from one another by gently dipping (1 to 2 degrees) erosion surfaces which truncate the more steeply inclined cross-strata. The stratification consists basically of two types: 1) low angle (less than 12 degrees) planar cross-stratification and 2) intermediate angle (12 to 20 degrees) trough cross-stratification which is locally abundant. Numerous burrows commonly result in mottling and irregular sedimentary structures (Fig. 5).

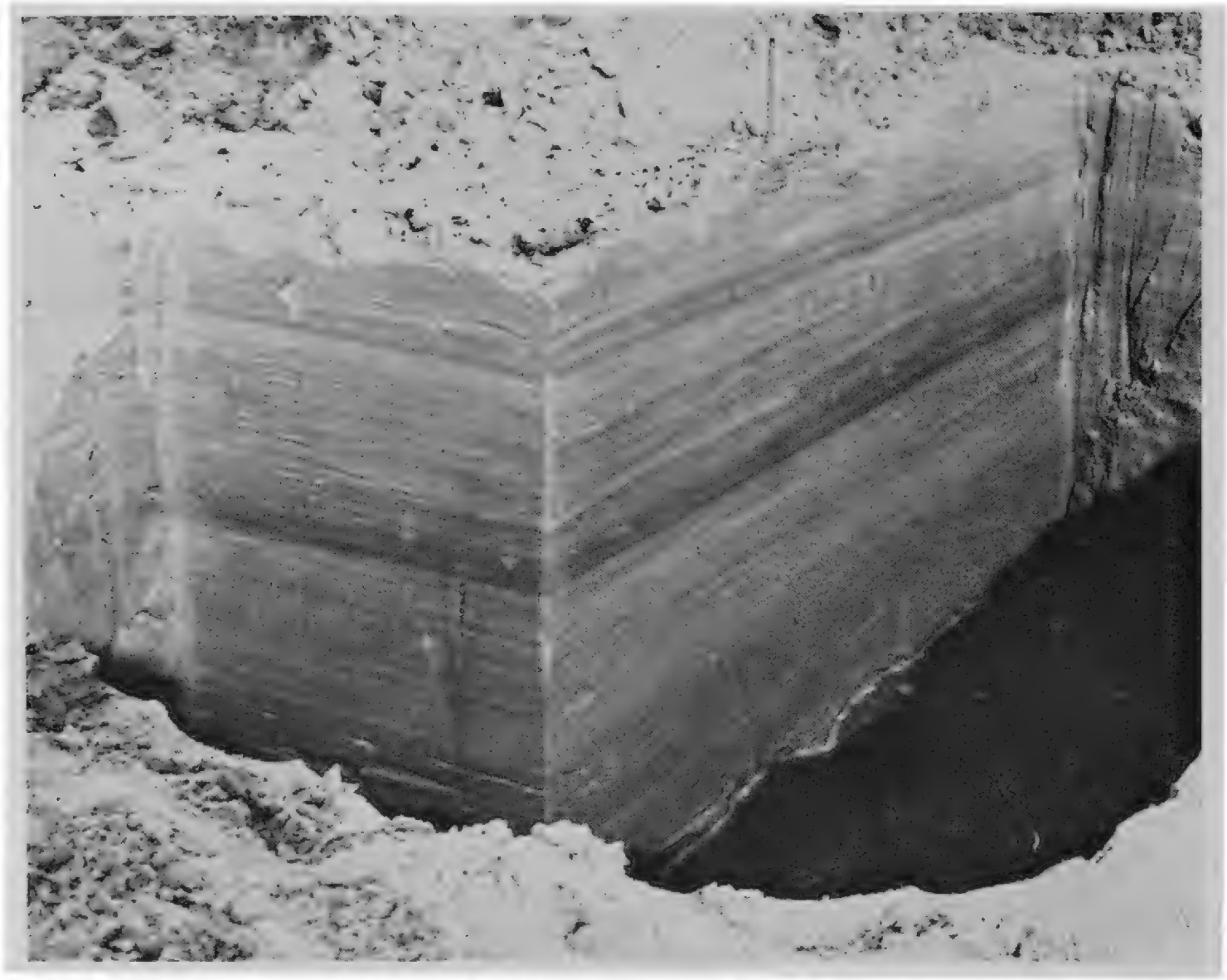

FIG. 4. Trench in upper foreshore at Station 1. Pencil is above face perpendicular to beach. Note parting surfaces developed along upper shoreface cross-strata near bottom of trench in face parallel to beach and burrow above them. The Gulf is to the upper right of the photograph.

In many instances, especially in the trenches of the backshore and dunes, dark grayish-black sand smelling slightly of hydrogen sulfide is encountered near the bottom of the trenches. The supper surface of this sand seems to coincide with the water table surface. The dark coloration probably is due to reduction of some material such as sulfates or organic matter below the water table, because after several hours exposure to the atmosphere the dark sand becomes much lighter and can scarcely be distinguished from the sands at the surface.

## WIND-SHADOW DUNES

The stratification of wind-shadow dunes is characterized by long (1 to 4 m), smooth, even, convexo-concave cross-strata. The individual cross-stratum in a longitudinal section consists of three elements: 1) near the top of the dune the cross-stratum is convex upward; 2) toward the leeward side it is straight along its mid-length; and 3) in its lower portion it is concave upward and is truncated by overlying cross-strata (Fig. 6). The sets are wedge-shaped, being thicker near the top of the dune and thinner leeward. Strata dipping at oblique angles to the predominant wind direction correspond to slip surfaces on either side of the crest of the dune tail. Apparent dips on these strata range

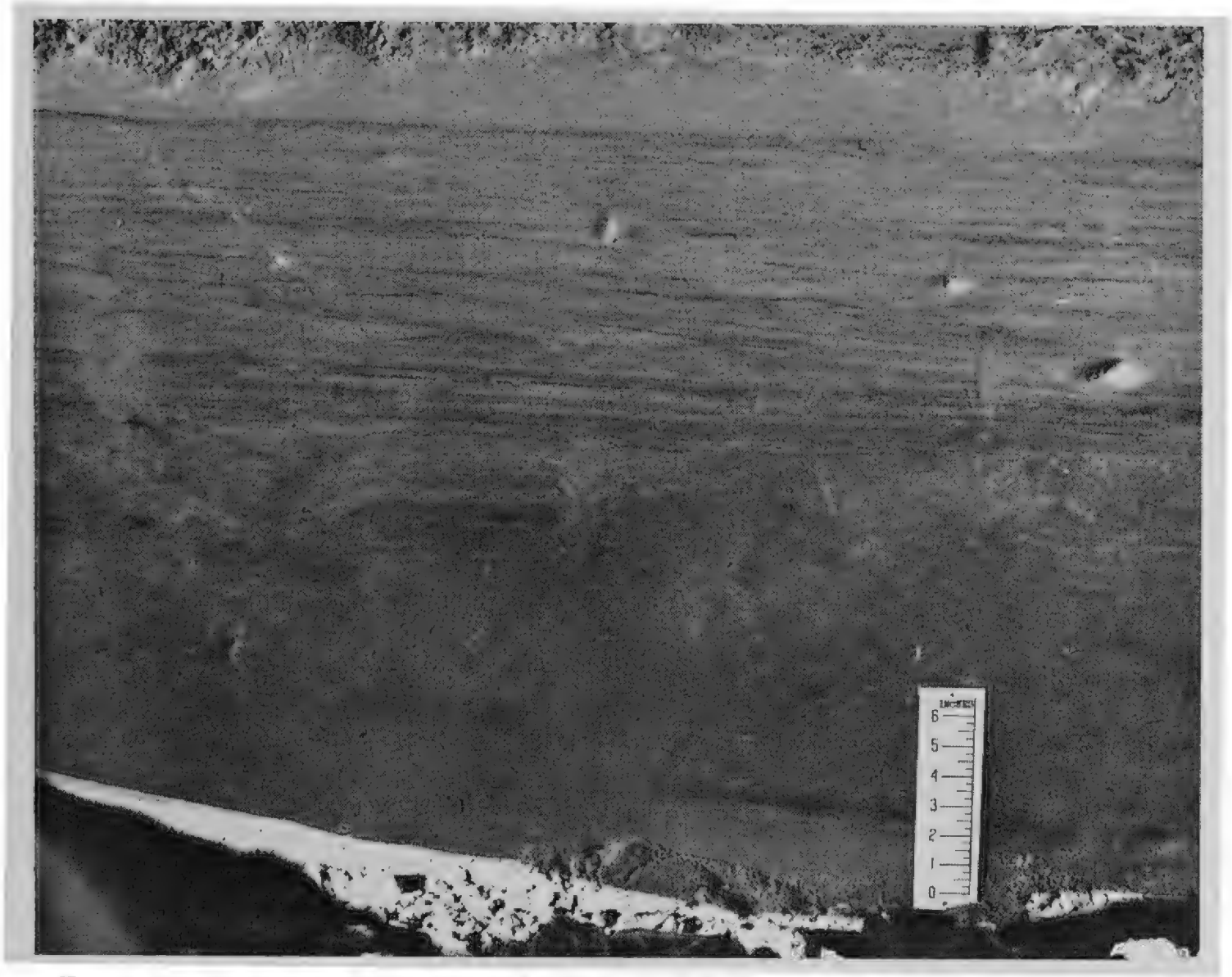


FIG. 5. Trench face perpendicular to beach in backshore at Station 2. Note set of low angle planar cross-strata dipping gently (2 degrees) seaward near top of cut, underlain by set of trough type cross-strata dipping 16 degrees seaward, underlain by set of gently dipping (2 degrees), planar cross-strata which in turn is underlain by massive to irregularly stratified and burrowed sand. Also note *Ocypode* burrow (in extreme left of photograph) filled with sand at boundary between set of trough cross-strata and lower set of planar cross-strata.

from 10 to 33 degrees. Vegetation made it impossible to observe stratification on the windward sides of these dunes. Thicknesses of individual cross-strata range from 0.1 to 4.5 cm and on the average are greater than those of the beach. The sets range in thickness from 10 to 66 cm.

In the lower portions of all trenches cut through the wind-shadow dunes, structures characteristic of the backshore were observed (Fig. 6). The maximum thickness of the eolian sand above the uppermost beach deposits varies between 1.5 and 2 m. In many places a layer of coarse shell material, similar to that observed covering some localities of the backshore (Fig. 7) is encountered at the base of the eolian sand.

## FOREDUNE RIDGE

The stratification of the foredune ridge is characterized by large scale, smooth, even, trough type cross-strata (Fig. 8). Apparent dips on the cross-strata range from 2 to 42 degrees. According to McBride and Hayes (1962, p. 547, Fig. 1) the direction of dip is bimodally distributed (WSW and N).

FIG. 6. Trench perpendicular to beach displaying longitudinal section through a wind-shadow dune at Station 1. Note relatively high angle, convexo-concave cross-strata dipping 10 to 19 degrees landward underlain by low angle, planar cross-strata of the beach facies dipping 1 to 3 degrees seaward.

The thickness of individual cross-strata ranges from less than 0.1 to more than 5 cm. Thickness of individual sets range from 8 to 45 cm, being similar in thickness to the sets of the wind-shadow dunes. Locally the cross-strata are disrupted due to roots and numerous animal burrows (Fig. 8).

## Discussion

Primary sedimentary structures such as those reported herein are basically a function of: 1) the characteristics of sediments being supplied (both mineralogic and textural); 2) the rate of supply; and 3) the types, intensity, and variability of the physical depositional processes. Because of the last factor, these structures are of special value in environmental reconstruction.

In the area studied, dominantly quartz sands are transported southwestward by long shore drift (Bullard, 1942; van Andel, 1960), and the rate of supply is not extremely variable. Therefore the primary stratification of these deposits is principally the result of periodic variations in the sorting ability and competence of the transporting medium. Furthermore, the beach environment is dominated by the energy released by physical

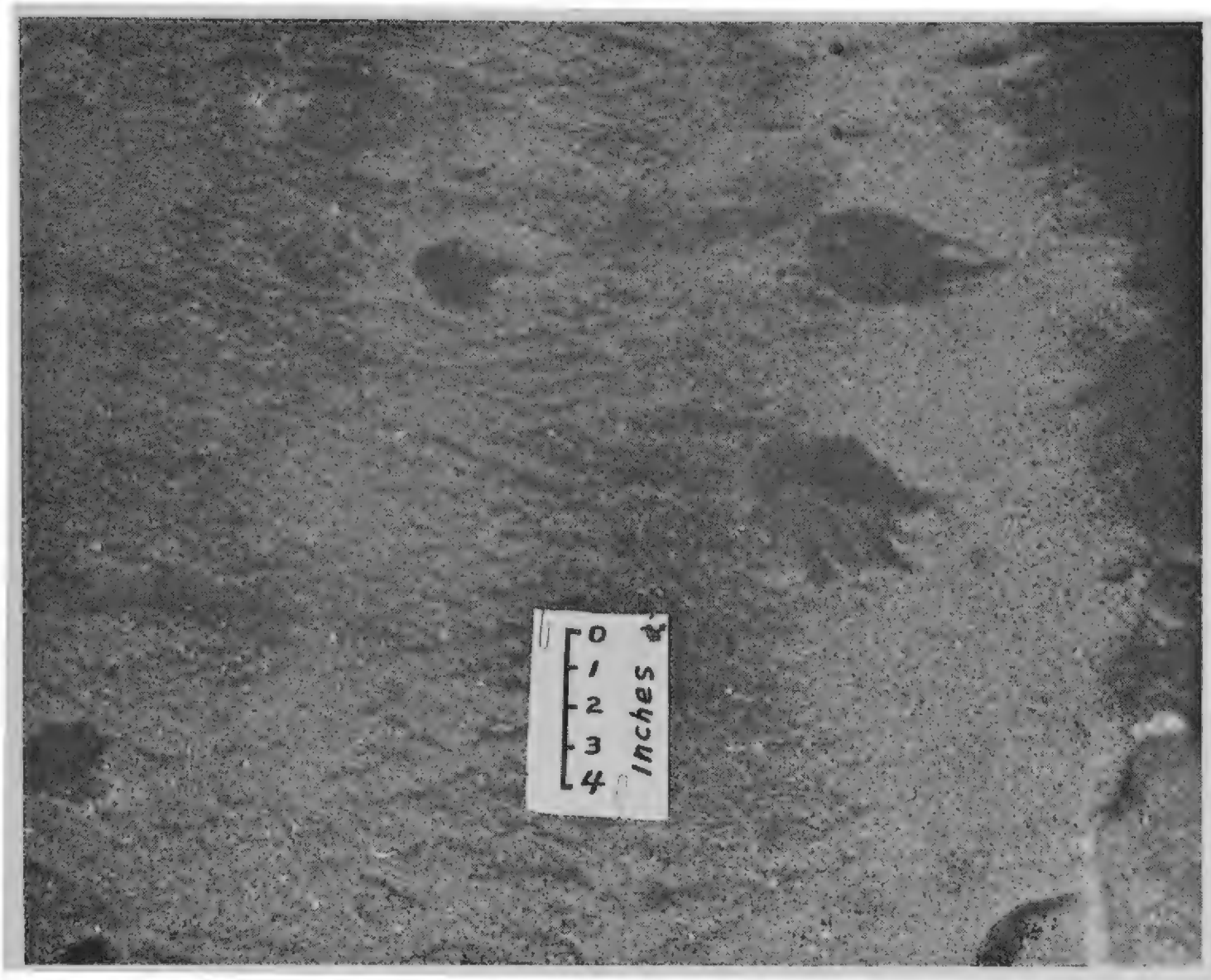


FIG. 7. Surface of extreme lower foreshore exposed at very low tide at Station 3. Note fine shell hash covering much of the surface, *Callianassa* burrows surrounded by small circular mounds of sand, and ill defined rhomboid "ripple marks" in center foreground. The Gulf is to the right of the photograph.

processes so that their effects—primary structures—predominate over secondary structures such as those produced by chemical diagenesis or burrowing organisms.

## FORESHORE

The stratification of the foreshore deposits conforms very closely to the configuration of the surface of this zone. It is concluded that the primary stratification results from wave action which can be seen continuously modifying this sloping surface. The wave energy varies directly with wind velocity and direction and thereby changes both daily and seasonally. The effects of these changes can be seen in the texture of mineralogically identical cross-strata. Size analyses show the sand of a relatively dark colored set of cross-strata to have a mean grain size diameter of 2.84ø (0.138 mm) and an inclusive graphic standard deviation of 0.33ø, while the corresponding values for a lighter colored set were 2.78ø (0.146 mm) and 0.35ø. The color discrepancy between the two sets is believed to be related to differences in moisture content and/or drying ability, since, when the samples were dried in the laboratory no color differences could be detected.

The regularity of the stratification is contributed to by the lack of ripple marks which

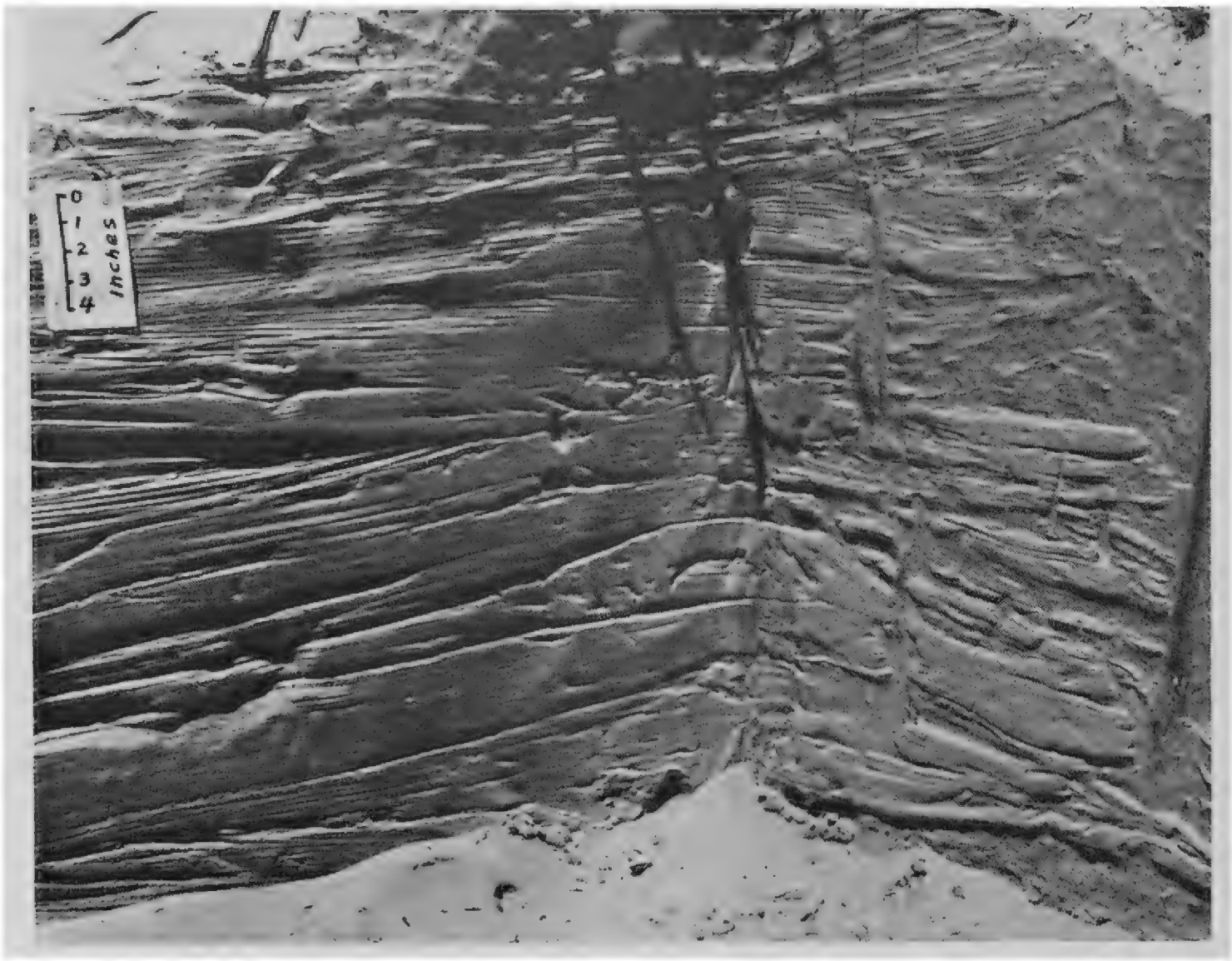


FIG. 8. Large scale trough cross-strata in trench near top of foredune ridge at Station 5. Scale attached to a root on trench face perpendicular to beach. The Gulf is to the right of the photograph.

generally form only on the extreme lower foreshore and upper shoreface and are exposed only at maximum low tide. Likewise marine organisms causing biogenic structures are restricted by the necessity for continuous submergence to the lower portions of the foreshore for the most part. They can extend up the foreshore to some extent, however, because the intertidal, beach community is entirely infauna and can subsist in interstitial water. This community is dominated by the pelecypod *Donax* which may be as abundant as 32,000 individuals per linear yard of beach (Loesch, 1957). However, the burrows of this and the other common mollusks (*Polinices, Terebra,* and *Oliva*) generally extend only a few centimeters below the surface, and wave action continuously reworks the sand destroying the secondary structures and replacing them with primary, regular stratification.

Burrows of a more permanent nature are made by the shrimp *Callianassa.* Most of the burrows are surrounded on the surface by a small circular mound of sediment (Fig. 7). They are commonly over 4 feet deep and are stabilized by an organic mucus which the animal secretes into the walls. When the sediment surrounding the burrow is eroded, the burrow will stand temporarily a few inches above the surface of the beach. The exterior of the burrow then reveals a characteristic knobby or coarsely corncob appearance. Although very few structures referred to burrowing organisms were seen in the foreshore trenches (Fig. 4), they are probably more common in the lower part of the zone where continuous saturation beneath the water table prevented trenching.

Deformational and cut and fill structures such as those reported by Emery (1945), Palmer (1948), and Soliman (1964) were not observed.

### Backshore

An observed sequence of events in the development of a backshore is depicted diagrammatically in Fig. 9. The backshore is periodically eliminated by hurricane tides which raise sea level until the shoreline reaches the foredune ridge which may then be deeply eroded. The whole beach, in effect then, becomes the foreshore and very probably develops primary, regular stratification. When the water recedes to its normal level, deposition occurs in the upper part of the intertidal zone creating a berm and redefining a backshore zone. Within this zone, then, the following processes take place.

1) Waves breaking over the berm crest at high tide carry sand landward and deposit it in regular, gently landward dipping cross-strata.

2) Water is temporarily ponded between the berm crest and the dunes. Ripple marks and consequent cross-strata may result when a) the berm is breached and the water flows back to the sea, or b) wind creates oscillation ripples in the standing water.

3) Terrestrial organisms such as the abundant ghost crabs (*Ocypode*) burrow into the sand; the abandoned burrows sometimes collapse to produce irregular structures and sometimes are filled with sand from above producing distinct mottles (Fig. 5).

4) Onshore winds winnow sand and silt from the surface leaving a lag concentrate of shell and other coarse debris (Fig. 10). The winnowed sand accumulates usually around vegetation and other obstacles forming wind-shadow dunes on the most landward portion of the backshore. These dunes often coalesce producing complex eolian cross-stratification. Northerly (offshore) winds redistribute part of this material seaward probably forming irregular or discontinuous strata on the shelly backshore surface.

5) Terrestrial vegetation invades the zone from the foredunes, and its roots tend to destroy primary structures and produce a more homogeneous sediment.

Subsequent high tides ranging from only slightly above average spring tides to full hurricane tides may destroy part or all of the results of these processes and begin a partially or completely new cycle.

### Foredune Ridges

The trough type cross-strata observed in trenches in the vegetated, stabilized foredune ridges along with their morphology and position are the same as for active dunes on other parts of Mustang and Padre Islands and thus clearly indicate a primary, eolian origin for the sedimentary structures. The presence of beach sands beneath the dune sand has been reported (Johnson, 1919; Price 1958; Bernard *et al.*, 1962), but the trenches studied were too shallow to verify this or to add other new data pertaining to the origin and development of this zone.

## Summary and Conclusions

The sands of the foreshore, backshore and dune deposits of Mustang Island are very similar both mineralogically and texturally. However, these zones may be differentiated locally on the bases of the percentages of heavy minerals (Bradley, 1957) and certain

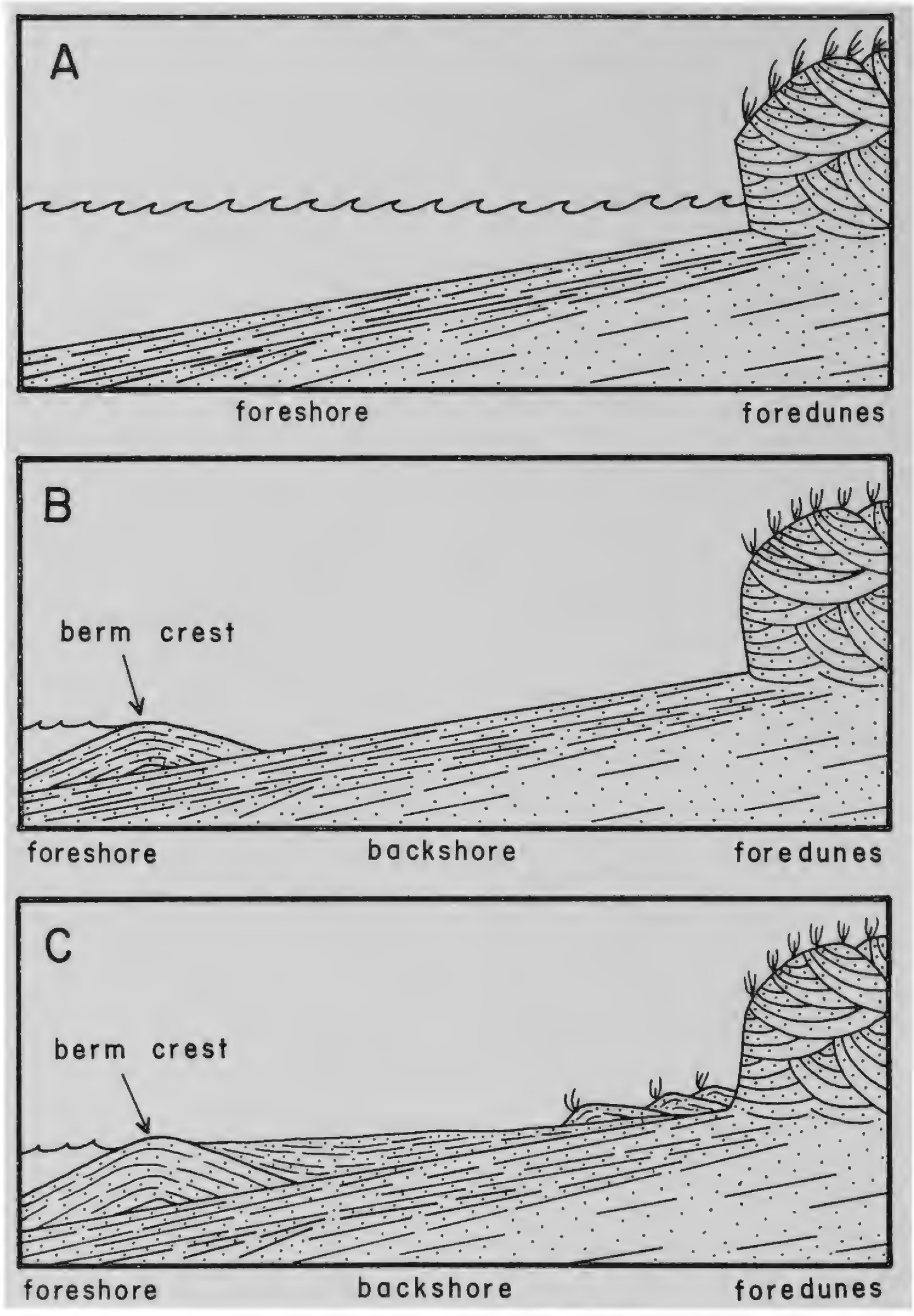


FIG. 9. Development of beach subsequent to a hurricane tide; A) hurricane tide reaches foredune ridge planing off entire beach into a foreshore; B) water level returns to normal, berm develops redefining a backshore; C) high tides and winds combine to fill in backshore and develop wind-shadow dunes.

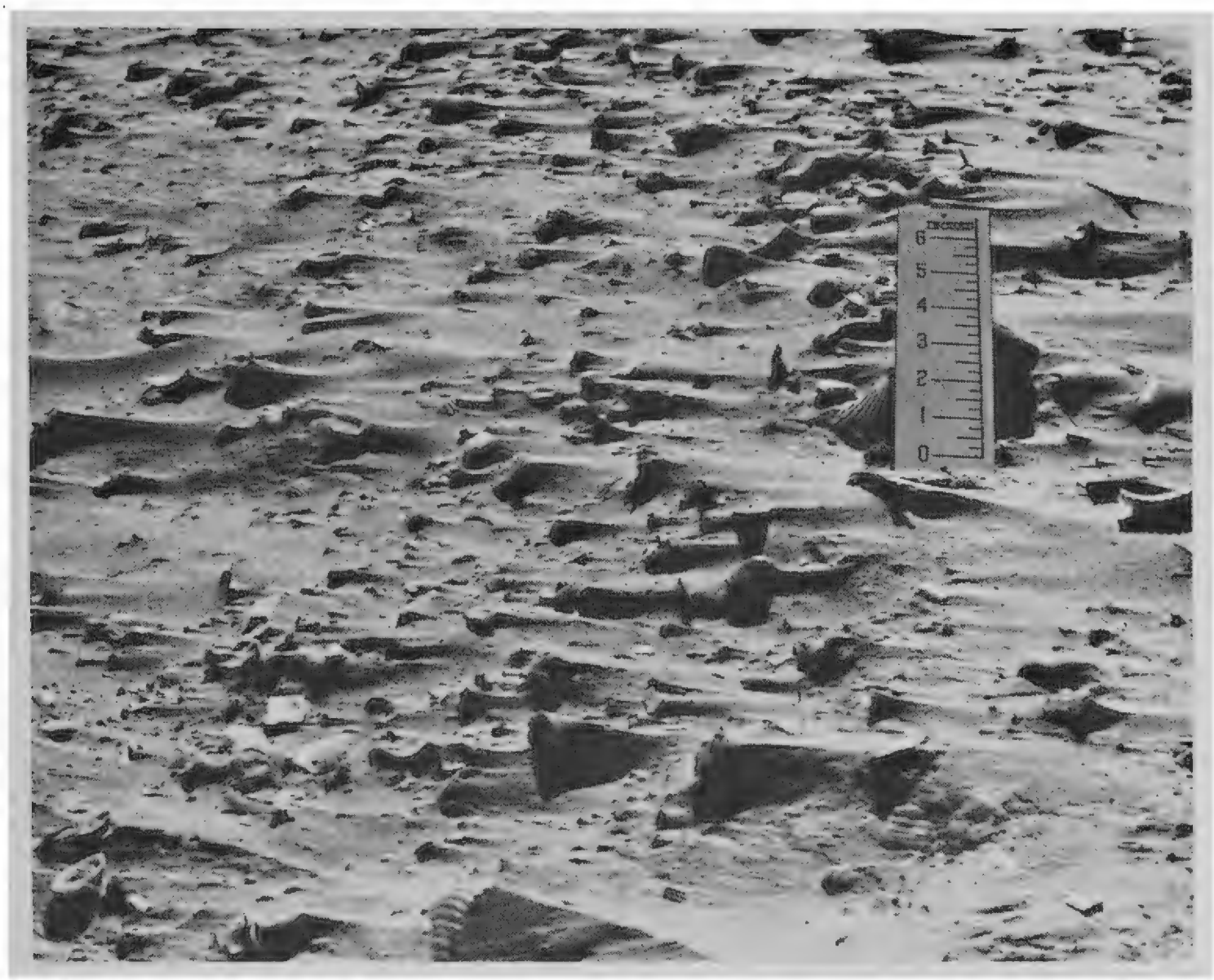


FIG. 10. Close up of lag deposit covering backshore surface. Note small tails of sand extending from the leeward side of the shells. The Gulf is to the left of the photograph.

textural parameters (Beal and Shepard, 1956; Mason and Folk, 1958). From data presented in this study and by McKee (1957) it has been shown that these zones can also be distinguished on the basis of their sedimentary structures.

The resulting sedimentary structures in each of the zones is determined chiefly by: 1) The agent of deposition, its competency and variability; 2) the form of the depositional or erosional surface upon which deposition takes place; and 3) the intensity of biologic activity. The stratification of the foreshore is principally the product of the sorting ability of the wave swash and backwash currents with relatively little modification by secondary agents. On the other hand, backshore stratification is the result of both wave and wind action with deposition at times on an irregular surface and significant modification by organisms. The dune stratification is predominantly the product of wind action with some modification by vegetation and burrowing organisms.

In each trench, surface material seems to be underlain by deposits of the next seaward zone. This vertical succession suggests an offlap sequence resulting from prograding of the shoreline. The succession observed, however, may also be the result of normal, sequential development of a beach following a hurricane tide. Further conclusions concerning beach growth and development must await the invention of better methods of sampling the water-saturated, unconsolidated sand deeped within barrier islands.

## Acknowledgments

We appreciate the assistance of participants in the 1964 summer field course on Marine Geology and Ecology under the direction of Professor Alan J. Scott, Mr. Peter B. Andrews, and Mr. Walter L. Siler, who helped excavate a number of the trenches reported here. The assistance of Professors Sherwood D. Tuttle and A. C. Trowbridge who critically read a preliminary draft of the manuscript and Professor William M. Furnish who offered several suggestions for reproduction of photographs presented in this study is gratefully acknowledged.

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# Growth and Mortality of the American Oyster, *Crassostrea Virginica*, in High Salinity Shallow Bays in Central Texas

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## Abstract

Mortality of oysters in a polyhaline bay on the central Texas coast was found to be massive. The dramatic decrease in oyster population during summer was attributed to the warm water (above 37C) and hypersaline (above 40 ppt) conditions. In spite of summer mortality, growth rates during fall and spring were exceptionally rapid. Spat was deposited during all seasons except in July through August.

## Introduction

South Texas is near the southern limit of the eastern oyster, *Crassostrea virginica* (Gmelin), and although it forms extensive reefs its existence seems to be marginal there. Temperatures and salinity fluctuate widely and much of the year temperatures are too high for good growth. Collier (1954) pointed out that oysters are surviving as a community dominant only in the northern Gulf of Mexico, and if an observed warming trend continues they may not even continue that status there.

The Port Aransas area is at about the southern limit of large reefs on the Texas coast partly because two very large hypersaline lagoons exist near the mouth of the Rio Grande. Breuer (1962) considered the oysters in South Bay, Texas at the Rio Grande mouth as a race especially adapted to high salinities. However, oysters grow in comparable high salinities in many other areas of the Atlantic and Gulf Coasts, but, they grow naturally in high salinities only intertidally as is true of the oysters in the vicinity of Port Aransas.

Actually, this is a simplification of the tidal situation, because the northwestern Gulf is unique in that seasonal changes in sea level are greater than average daily changes. There are spring and fall highs and winter and summer lows with differences of about 0.3 m (Marmer, 1954). Therefore the tidal zones change four times a year with dry land becoming covered with water and shallow areas becoming uncovered. Furthermore, tides are mixed and frequently are overcome by strong winds (Collier and Hedgpeth, 1950).

It was our intent to examine several oyster reefs through the period of these sea level changes, and record the effects of an environment which may be considered as more rigorous than normal intertidal zones. Despite these rigors, oysters were common in the study area and seemed to exhibit extremely fast growth. Compensating for this seemed to be a short life span, with perhaps less than an annual cycle.

[1] Present address: University of Georgia Marine Institute, Sapelo Island.

### Methods

Four oyster reefs in Redfish Bay and Harbor Island (Fig. 1) were visited irregularly between February 1964 and July 1965. Observations on the reef adjacent to South Harbor Island were discontinued when strong onshore winds held the water away from the oysters until they died.

A "semi-random" sampling technique was employed. A square-meter frame was dropped at five pre-determined places on a transect selected at random. The first square-meter was always at the top of the reef and the fifth was near the edge of the reef. All oysters within each frame were counted and the first 100 encountered on each reef were measured. Salinity, temperature of water and mud, water depth, evidence of recent mortality, presence of predators, presence of spat, general conditions of the reef and other factors were recorded. Salinity was determined by titration (Mohr method) or with a Goldberg refractometer (Behrens, 1965).

Oysters were taken from Hog Island and Steadman Island reefs for measurements of shell lengths and meat weights. Wet weights were determined on the meats after they were removed from the shell and the excess water blotted.

## Description of the Reefs

The first location is in a small cove off South Harbor Island (Fig. 1). There is no well defined reef, but numerous small oysters in clusters up to about 1 meter in diameter are found over most of the flat. Water depths never exceed 0.5 m up until April, 1964 when all the oysters died because of exposure.

The second location was a reef of moderate size adjacent to Steadman Island and partly interspersed with red algae and shoalgrass, *Diplantheria wrighti* (Fig. 1). This is the only reef studied which is fished by man. It is adjacent to the Port Aransas causeway and many oysters are removed by man in February, March and April.

A small reef on the north end of Hog Island (Fig. 1) provided the third location. Adjacent to the reef are beds of shoalgrass and algae.

The fourth location is within the tidal salt marsh of Harbor Island (Fig. 1). The reef is poorly formed inside a nearly silted tidal channel. The largest oysters are typical coon oysters adjacent to *Spartina* clumps and many are partially buried.

Profiles of the two major reefs (Steadman Island and Hog Island) are shown in Fig. 2. At mean sea level, 85% of Steadman Island Reef and 15% of Hog Island Reef are exposed. However, because of their location, strong prevailing (SE) winds push water over the reefs during times of low water. There is considerable mortality on these reefs during late summer because of the low water levels, calm weather and high temperatures characteristic of that period.

## Results

Numbers of oysters per square meter, average shell length, temperature, and salinity are plotted in Fig. 3.

Lowest temperatures recorded were 15.8 to 16.2 C, but it must have been much colder. During "blue northers," water temperatures approach 0 C, as is true of all shallow Texas

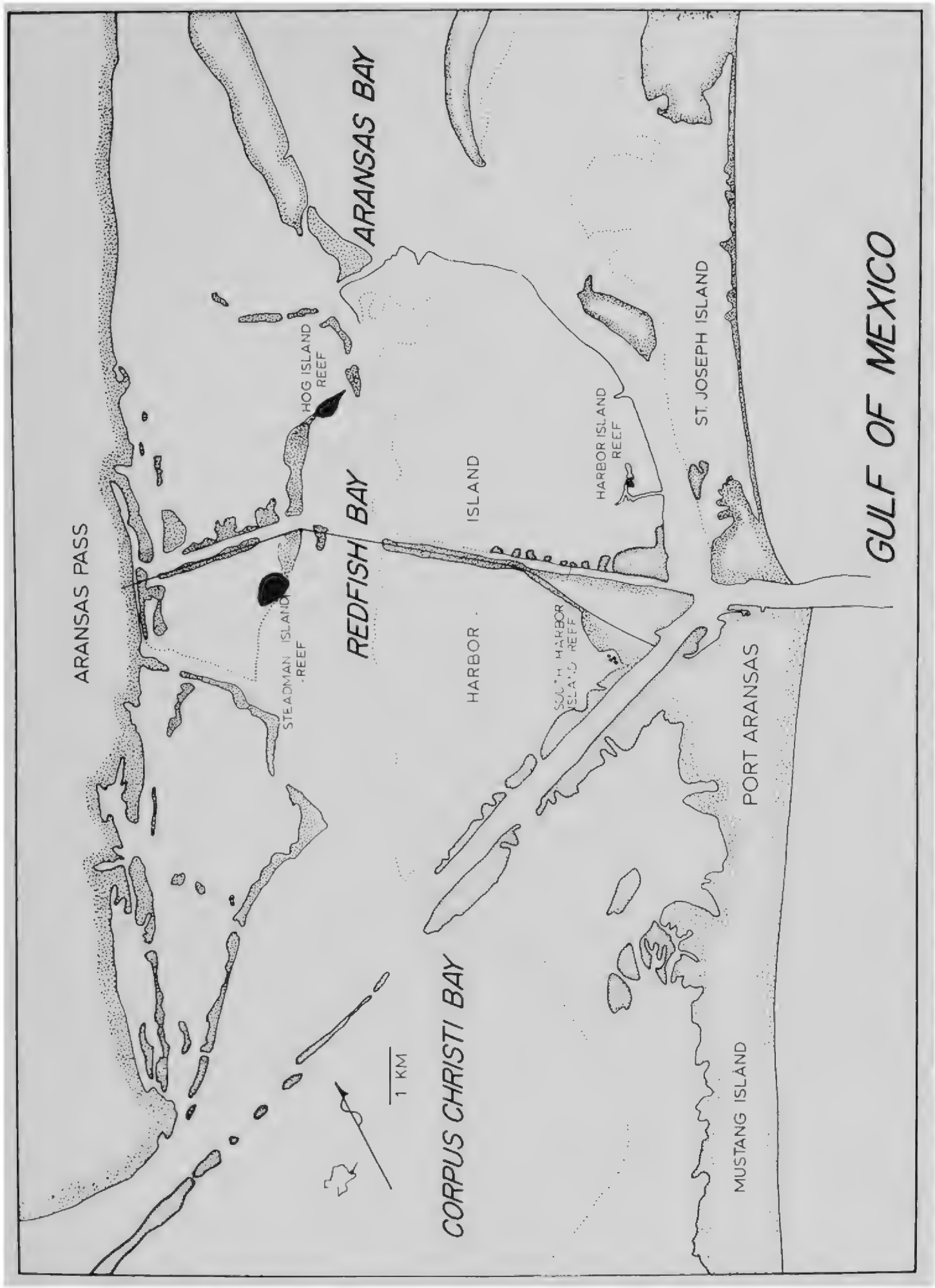


FIG. 1. A diagram of the Redfish Bay area of the Central Texas coast. The arrow indicates the relative area on the Texas coast. The four reefs considered in this study are indicated in black.

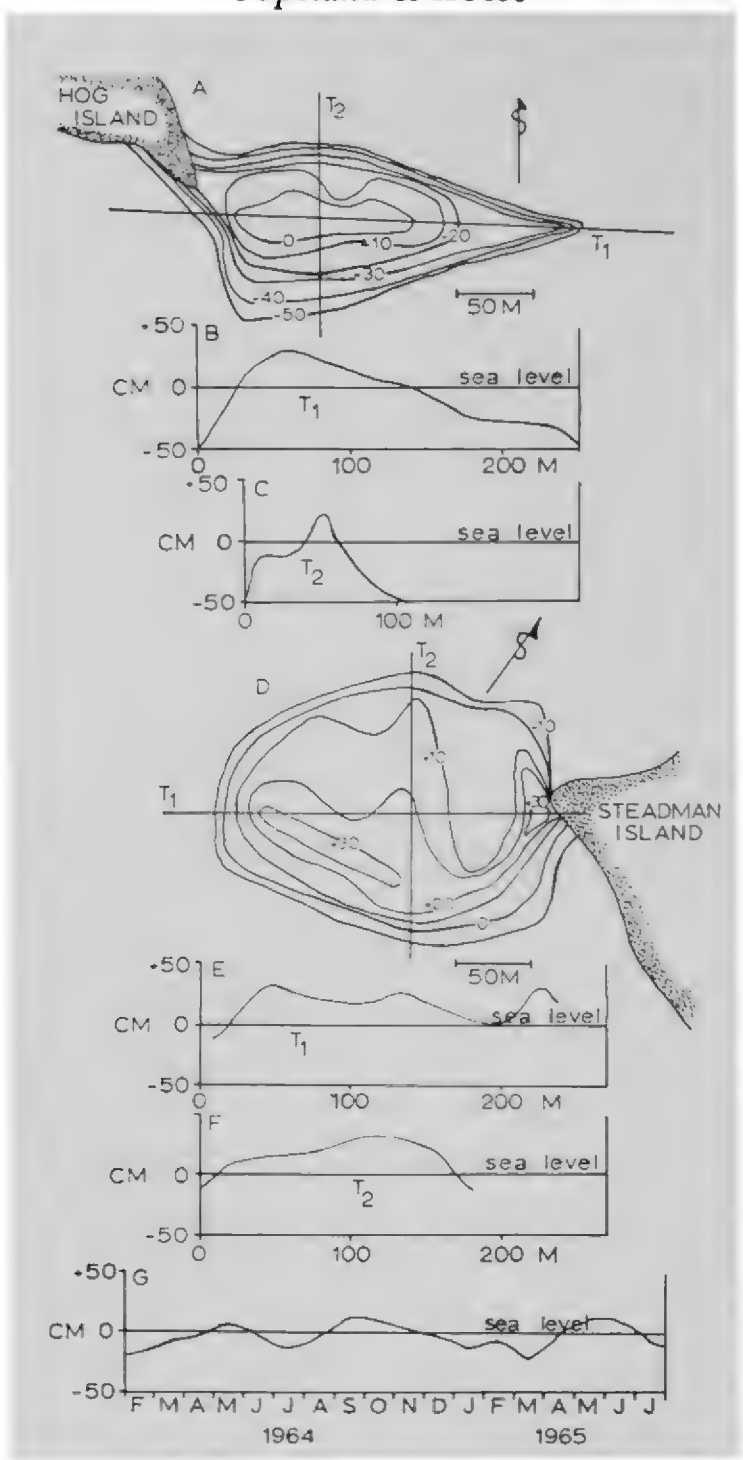


FIG. 2. Profiles of the two major reefs and mean water level during the study period. The horizontal line labeled sea level on each graph represents *mean* sea level as based on U.S. Coast and Geodetic Survey Markers. A. Contour drawing of Hog Island reef. Each contour is ten cm higher than the one just outside it. The zero contour is mean sea level; B. A profile along the length of Hog Island reef ($T_1$); C. A profile across Hog Island reef ($T_2$); D. Contour drawing of Steadman Island reef. Each contour is ten cm higher than the one just outside it. The zero contour is mean sea level; E. A profile along the length of Steadman Island reef ($T_1$); F. A profile across Steadman Island reef ($T_2$); G. Mean monthly water level in Aransas Bay (adjacent to Redfish Bay) during the study period. Each monthly level is the mean of daily values. (These data are courtesy of U. S. Coast and Geodetic Survey, Washington, D. C., Mrs. Martha A. Winn).

waters (Collier and Hedgpeth, 1950). The highest temperature was 38.0 C at Steadman Island reef, 35.0 C at Hog Island and 34.0 at the Harbor Island reef. The latter reef probably never reaches the extreme temperatures of the first two because the oysters are partly buried and it is located in close proximity of the ocean. Temperature of the mud of the first two reefs was often 2 to 3 C higher than the water, presumably because of the black surface absorbing heat.

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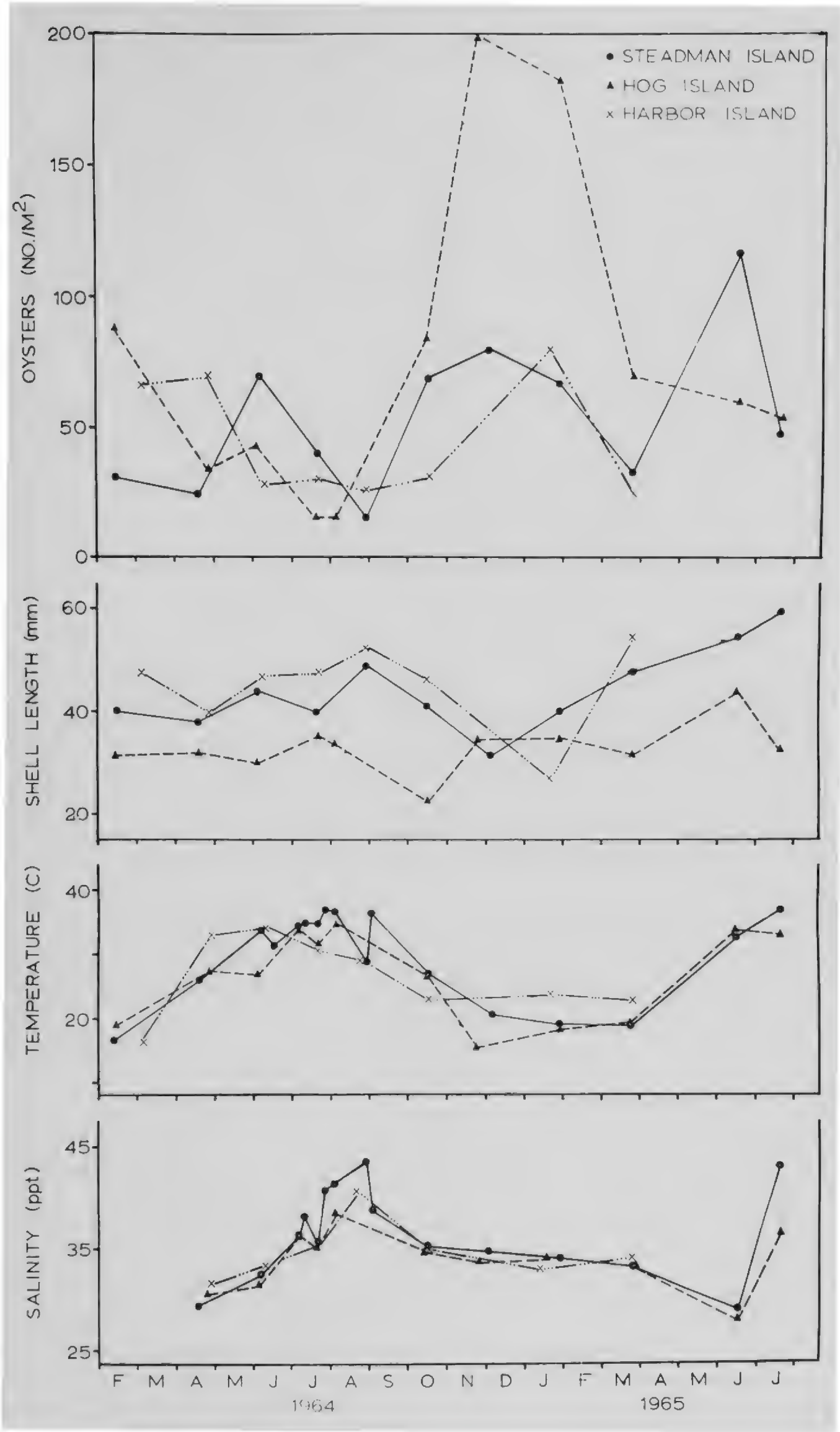
FIG. 3. Number of live oysters per square meter (each point is a mean of five counts), length of shell (each point is a mean of the first 100 oysters encountered), water temperature, and salinity at each reef during the study period.


STEADMAN ISLAND
HOG ISLAND
HARBOR ISLAND
OYSTERS (NO./M²)
SHELL LENGTH (mm)
TEMPERATURE (C)
SALINITY (ppt)
F M A M J J A S O N D J F M A M J J
1964
1965

Salinity varied between 28.0 and 43.5 ppt, but the range of the Harbor Island reef was less than the other reefs, again due to the proximity of the ocean. Oysters of the Central Texas coast probably grow in as high salinities as they do anywhere. In areas to the south of Corpus Christi, salinities of over 45 ppt are common (Behrens, 1966), and oysters are absent; suggesting that such values limit the distribution of the animal.

Sea level varied sharply with the seasons, exhibiting the usual spring and fall highs and summer and winter lows. Average sea level by month for Port Aransas is shown in Fig. 2. This was often modified by wind systems, as will be discussed later.

The numbers of oysters at the 3 stations were erratic, but generally the lowest populations occurred during August and the largest in spring and fall. Populations varied between 15 and 200 per square meter. Again the extremes (25–80) at Harbor Island were less than at the other reefs.

The average size was dependent on the number of spat present. At the Steadman Island reef size ranged between 31 and 60 mm, at Hog Island between 22 and 44, and at Harbor Island between 27 and 55. The average size was greatest in summer when spat were scarce and was least when spat became common in fall (Fig. 3).

The weight of oyster meats were computed from a sample taken on 15 February 1965 and is plotted against shell length in Fig. 4. Weight ranged between 0.03 and 7.80 g, and length between 13 and 70 mm, as great a range as was found during the study. The relationship between oyster meat weight and shell length was curvilinear on a semilog plot.

The meat weight from Fig. 4 was applied to the size of oysters noted in the field observations. The weight of meat as interpolated from average size was multiplied by the average number of oysters per $M^2$ to obtain the biomass on each reef (Fig. 5). This results in an error due to seasonal changes in condition (Gunter, 1942), but for our purposes gives a suitable estimate of biomass. Biomass ranged between 31.2 and 478.9 $g/M^2$ at the Steadman Island reef; at Hog Island 8.4 to 165.2 and at Harbor Island between 20.6 and 194.1. The greatest biomass as Steadman Island occurred in late spring both years, while it was erratic the rest of the year. On Hog Island reef, the biomass was fairly low during the spring of 1964 but higher during the spring of 1965. The greatest biomass occurred during the winter on Hog Island Reef and the least during the summer. There was not as much variation in biomass on the Harbor Island Reef as in the other two reefs. However, the largest biomass occurred during spring of both 1964 and 1965 and the lowest biomass during the winter of 1964.

## Mortalities

During July and August 1962 and 1963 several days of coincident low tides and high afternoon temperatures of 38–39 C caused significant mortality. In late August and early September several trips were made to all known oyster reefs in Redfish Bay and a few inside the salt marsh at Harbor Island. No live oysters were found on any of the Redfish Bay reefs. None of the associated animals (crabs, fish, mussels, barnacles) were found alive.

Live coon oysters partly buried in silt in Harbor Island were not rare, although no counts were made.

In 1964 and 1965 mortalities were less, but all oysters on the top 10 cm of Steadman Island and Hog Island reefs died in July and August. At Hog Island on 20 July

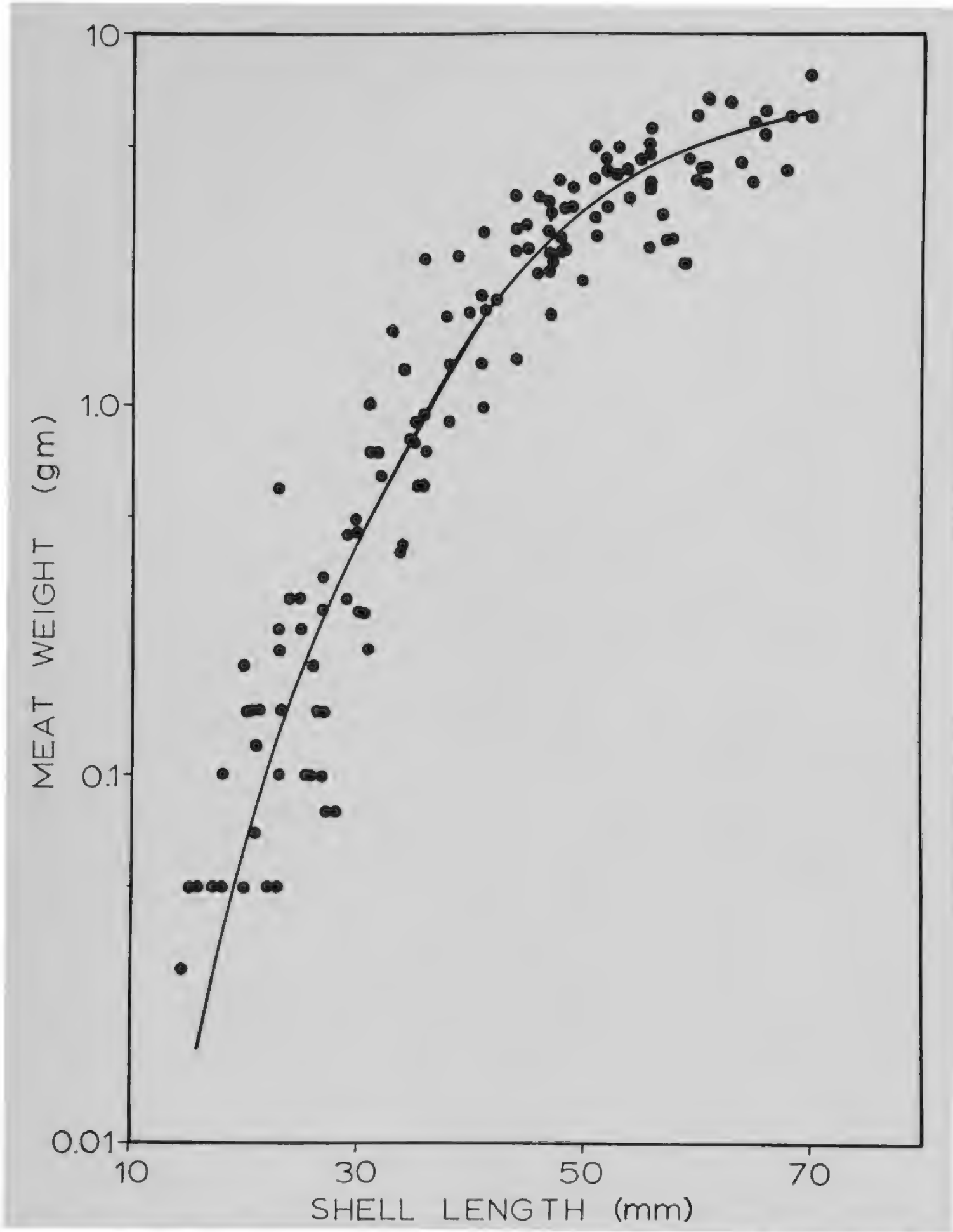



FIG. 4. The weight of oyster meat versus the length of its shell for 165 oysters from Steadman Island reef on 1 Feb. 1965.

1964 recently dead and weak oysters were found. Nineteen oysters from 25 to 60 mm in length were found with either portions of meat or muscle left. Several recently dead or weak *Anomia simplex* were found.

At South Harbor Island by 19 April, 1964 no live oysters were left, and there were many in various stages of decay. Strong, continual SE winds (15–25 kts) had blown

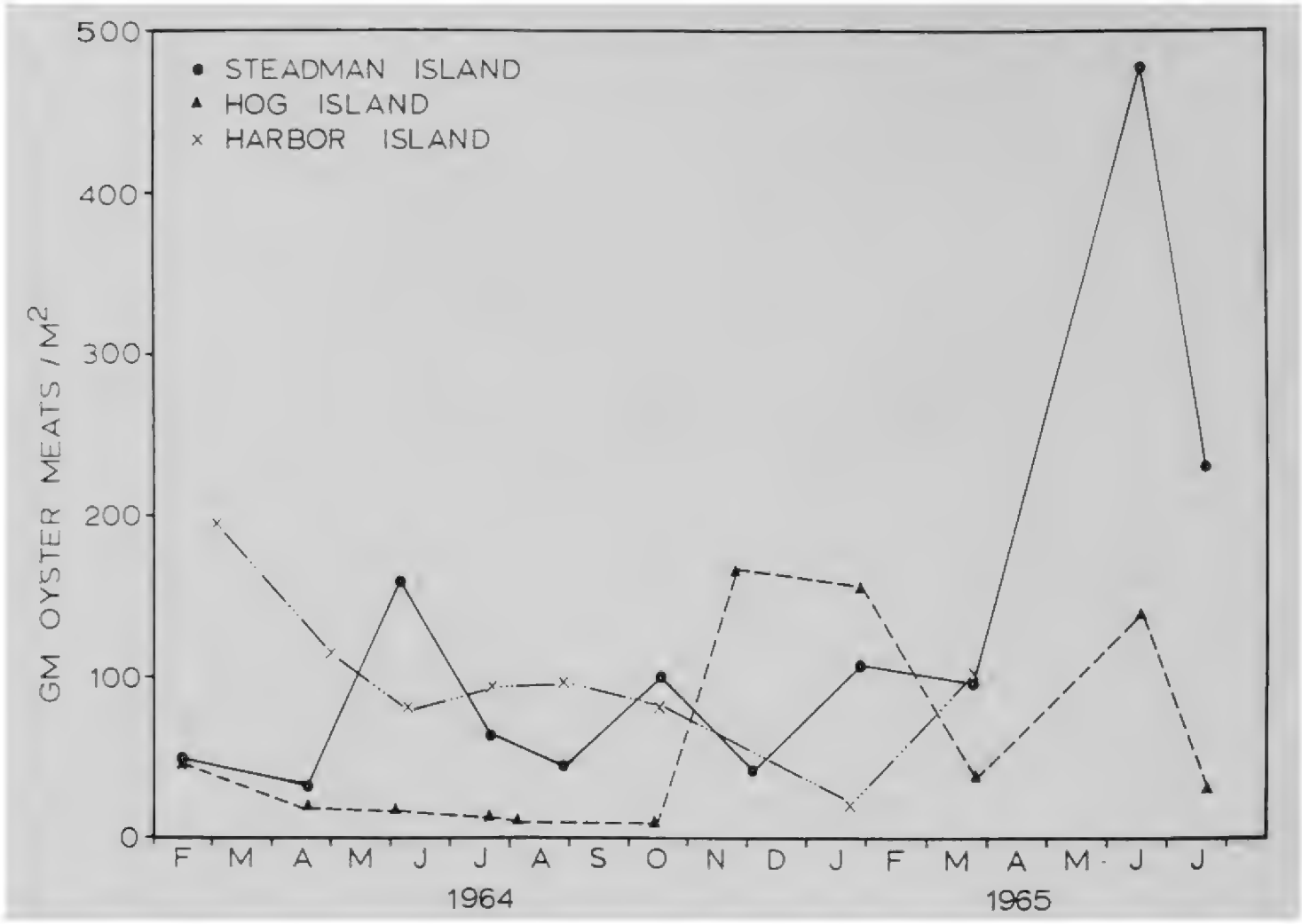



FIG. 5. The amount of oyster meat per square meter on each reef during the study period. Each point was computed by multiplying the average meat weight for the average shell length (from Fig. 4) by the average number of oysters per square meter.

for the previous two weeks and no water had covered this flat at any tidal stage. Growths of *Salicornia* had invaded the area between 5 March and 18 April, but judging from the size of the plants and casual observation of the tides, this did not begin until April.

## Discussion

There seems to be two separate types of refs present in the area. The first consists of the well defined reefs in Redfish Bay, which are composed of predominantly small oysters. Population size fluctuates rapidly, reaching its greatest density in winter and its lowest in summer when tides are lowest and salinities and temperatures highest. There was no evidence that salinity was responsible for the fluctuations in numbers, but the effect of summer hypersalinities coincides with other adverse factors. High temperature and dehydration were undoubtedly responsible for some of the catastrophic mortalities. Although we are not able to rule out disease, the fact that all sizes were affected indicates a physical cause of death (Mackin, 1961).

Galtsoff (1964) reported internal temperatures of 46 to 49 C in exposed southern oysters and he noted that at about 32 C, ciliary movement rapidly declined. The air and water temperatures measured in Redfish Bay were high enough, however, to suggest that extremely high internal temperatures were reached (Fingerman and Fairbanks, 1957). Whether these high temperatures will oysters outright or allow parasites or diseases to do so cannot be proven with our data.

It seems that, although severe summer mortalities occur, it is exceptional for them to

be total as apparently occurred in 1962. Mortality on the tops of these reefs may however always be total. Apparently several days of extremity low, afternoon tides must coincide with very hot days. In 1964 and 1965, either storms, rain, wind, or cloud cover prevented these conditions from existing. Thus, only a single factor can seemingly prevent total mortality. There are only a few days each summer when low tides occur during the hottest time of day, and these seem to be the key to the mortalities. Even so, the low summer stand in sea level allows severe, if not nearly total, mortalities most years especially high upon the reefs. Other factors of possible influence include yearly differences in sea level (Marmer, 1954) and yearly variation in local wind systems.

The biomass data presented in Fig. 5 substantiate the impression that growth occurring on oyster reefs in this area, especially during spring is uncommonly rapid. Disregarding maintenance, mortality and shell construction, net oyster meat production was 5.2 gm $m^{-2}$ $day^{-1}$ between March 24 and June 16, 1965 on the Steadman Island reef. Lesser, but still significant, growth was evident during the spring (2.7 gm $m^{-2}$ $day^{-1}$) and fall (1.4 gm $m^{-2}$ $day^{-1}$) of 1964 for Steadman Island reef, during the fall (3.8 gm $m^{-2}$ $day^{-1}$) of 1964 and spring (2.0 gm $m^{-2}$ $day^{-1}$) of 1965 for Hog Island reef, and during the spring (1.3 gm $m^{-2}$ $day^{-1}$) of 1965 for Harbor Island reef. During other times of the year, maintenance and mortality exceeded production and net production was negative (total reef oyster meat biomass decreased).

Predation seemed to be relatively light. Some crab predation was evident, but there was little evidence of predation by other animals in the shells of dying or weak oysters. Oyster drills, *Thais haemastoma*, were absent in the study area, and have been found only at the edge of the ship channels.

Despite the high mortality oysters are often common and growth rate seems exceptionally rapid. Most surviving spat fall seemed to occur after the hotter summer months, and although oysters were very common in the winter their biomass was small. By May the biomass had increased due to growth. This seemed to be the general pattern at all reefs although it was somewhat obscured at Hog Island, especially in the spring of 1964. This is essentially the pattern of Louisiana oysters (Hopkins, Mackin and Menzel, 1954), which are at their best condition in spring.

Although a few oysters survive the summer, there is little evidence that 2 year old oysters compose any but an insignificant part of the population. For this reason the area may never produce large amounts of oysters, but could, with proper management, produce seed to be removed in late spring or early summer.

## Acknowledgments

The facilities of the Institute of Marine Science, Port Aransas, Texas, were utilized during the study. Messr. Bill Gillespie, Frank Moseley, Michael J. Canoy, David L. Steed, Douglas Hoese, E. D. Lane, and John Miller, Mrs. Jean Copeland, and Mary Van Nortwick assisted with laboratory and field work. Mr. Bill Gillespie constructed Figure 1.

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# A Study of Production and Phosphate in a Sonoran Lagoon[1]

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## Abstract

Measurements of community metabolism, plankton production and phosphate were made in four interrelated environments of a hypersaline lagoon system. Gross production of freely circulating water, diminished inward ranging from 12.2 g $m^{-2}$ $day^{-1}$ near the tidal entrance to 0.7 g $m^{-2}$ $day^{-1}$ in an ephemeral deadwater near the head. These variations reflect a headward increase of turbidity and the activity of different types of producers. In the central lagoon potentially rapid photosynthesis is diminished by high turbidity leading to a near balance between gross production and community respiration.

Total phosphate reached 10.1 μg-at/1 at the head—eight times greater than concentrations in supplying gulf water. Diurnal variations of inorganic and dissolved phosphate associated with metabolism varied within narrow limits. Most distributions of total phosphate paralleled "turbidity." Accumulation near the head is attributed to inward transport of suspended particulate materials.

## Introduction

Along the central eastern shore of the Gulf of California, margins of the coastal plain are indented at the mouths of dry rivers and partly drowned by gulf water (Fig. 1). Estero Tastiota, like many lagoons on the Sonoran coast, is a shallow reentrant protected from open-gulf wave action by a barrier spit.

The lagoon is alternately flooded and drained by the tide which ranges about 0.6 m. This action mixes lagoon water with gulf water and is a means of carrying particulate materials into or out of the lagoon. Superimposed on the oscillatory movement of the tide there is a small inward net or residual flow from the gulf to renew lagoon water lost by evaporation. Circulation of lagoon water and the chief physiographic elements are diagrammatically illustrated in Fig. 2E. Postma (1965) showed how high water temperature in an arid coastal lagoon may cause a reversal of typical "antiestuarine" density flow.

Lagoon water in the estero is hypersaline most of the time, owing to infrequent drainage and high evaporation. Salinity increases with distance inward from the entrance, reaching about 41 ppt at the head (Fig. 2A). Farther inward, beneath exposed pans and high flats surrounding the inner lagoon, dissolved salt concentrations of interstitial "ground" water exceed an estimated 200 ppt. These salts are drawn upward by capillary action and precipitated in nearsurface sediments as the water evaporates, a process reported by Oppenheimer and Ward (1963) in Texas bays.

Desert winds that sweep the lagoon surface generate local waves capable of stirring up bottom muds including benthic algae and detritus. Visibilities measured by Secchi disk decrease inward, ranging from about 400 cm off the lagoon entrance to 6 cm in the inner reaches. The depth of light penetration may be expected to show a corresponding inward

[1] Contribution No. 221 from the Virginia Institute of Marine Science. This study was accomplished at the University of California.

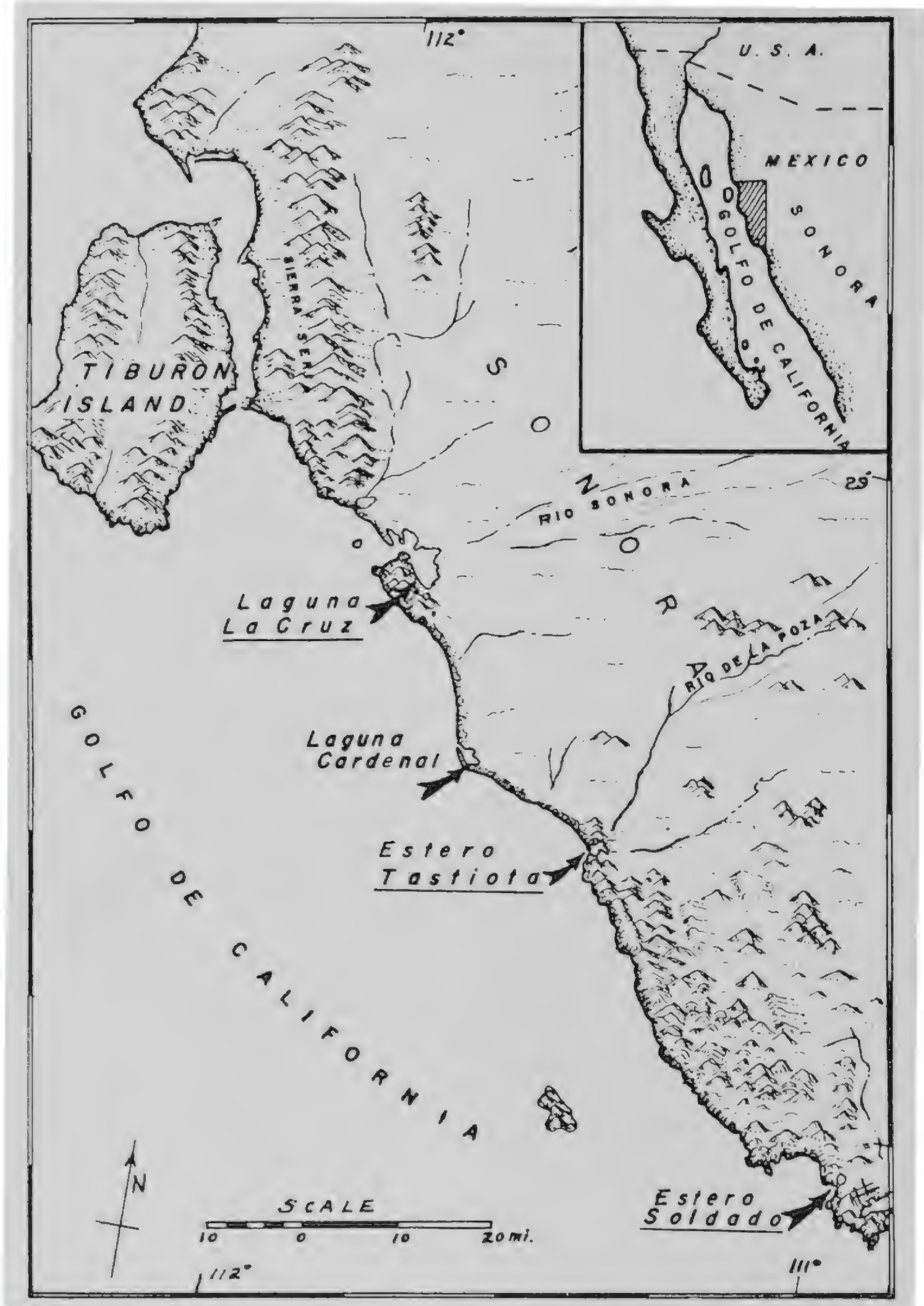


FIG. 1. Location of lagoon systems on the arid Sonoran coast of Mexico.

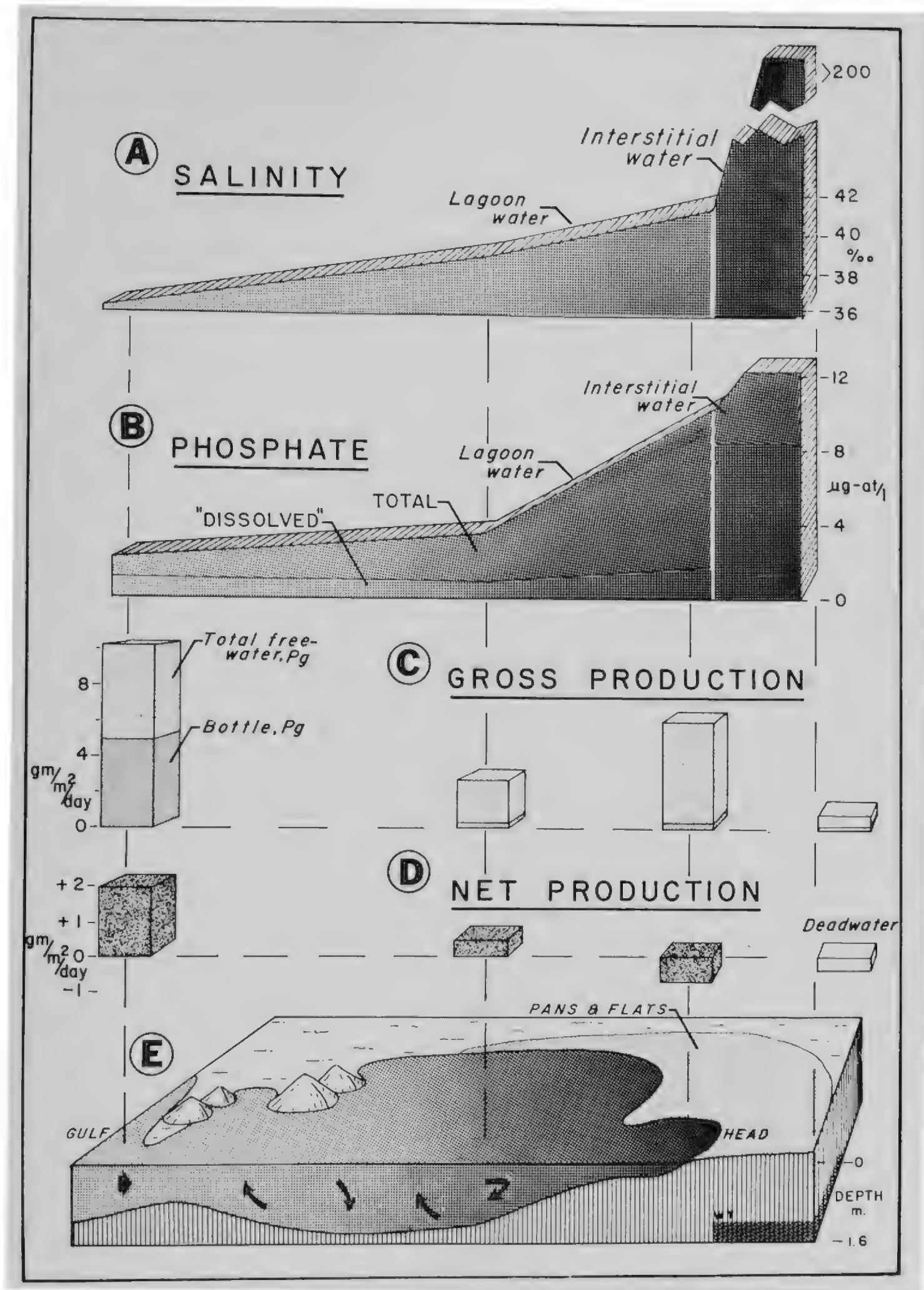


FIG. 2. Horizontal distribution of chemical properties and organic production in a schematic lagoon system. (A) Average concentration of salinity in lagoon and interstitial water at Estero Tastiota, April, 1961. (B) Average concentration of phosphate fractions with distance headward at Estero Tastiota, April, 1961. (C) Average rates of total free-water gross production including the "bottle" increment, in different areas of Estero Tastiota. Averages are based on data of Table 1. (D) Average rates of free-water net production in different areas of Estero Tastiota. Averages based on data of Table 1. (E) Schematic diagram of Estero Tastiota showing circulation (arrows), and major physiographic elements. WT—water table.

diminishment. Material that is churned up in the central lagoon tends to settle out and accumulate in quiet-water embayments and at the head.

Organic material is synthesized in the lagoon by three types of producers; each inhabits different but interrelated environments of the lagoon system. Benthic algae flourish on the high flats and pans when flooded during summer spring tides; whereas, phytoplankton is important in the nearshore gulf. *Zostera*, a benthic grass, is the chief producer of the central lagoon but in winter it is partly replaced by abundant growths of *Enteromorpha*.

Sedimentation is slowly filling the lagoon depression with land-derived mud. Sediments are supplied to the lagoon mainly by local sheetfloods or by spasmodic flooding in river channels that converge into the tidal area. Although runoff is infrequent under the arid climate of today, there is substantial historical and archaeological evidence (Ives, 1953) that the climate of the region was wetter in the recent past. The lagoons are backed by a terrain of basic volcanic rocks—a potential source of phosphorus in soils of the region. Sediments of the high flats bordering the lagoon are oxidized (+95 to +590 mv Eh) but in the central lagoon they are reduced (0 to −195 mv Eh) and anaerobic beneath a thin oxidation layer. The reduced condition permits regeneration of phosphate-enriched sediments supplied to the lagoon.

This paper describes the distribution of phosphate and the rates of organic production in an arid coastal lagoon. An attempt is made to identify processes active in the supply and circulation of phosphate which operate in combination with energy factors to determine the long-term accumulation of organic matter. The study was concentrated at Estero Tastiota, a remote and unpolluted lagoon with a broad range of transitional environments. The small size of the lagoon, 3.5 km$^2$, permitted numerous one-man observations at closely spaced intervals.

## Procedures

Phosphate concentrations of water and sediment samples were determined by the method of Robinson and Thompson (1948). For total phosphate the samples were digested with perchloric acid prior to colorimetric analysis with stannous chloride and ammonium molybdate. Inorganic phosphate was determined after a 3-minue reaction with acid molybdate and the "dissolved" phosphate was determined after removal of particulate material on a membrane filter. Estimates of total organic production were accomplished by the free-water diurnal oxygen curve method of Odum and Hoskins (1958). Most water samples were taken during neap or mean tide to avoid the effects of oxygen advection by tidal action. Dissolved oxygen concentrations were determined by the Winkler method on samples collected at two to three depth intervals and at several stations for a 24-hour period. Rates of gross production and respiration were determined graphically after correction for diffusion between air and water as outlined by Odum. Metabolism of suspended material, chiefly phytoplankton, was estimated concurrently at each station with ordinary light and dark bottles.

## Results of Observations

Concentrations of total phosphate at Estero Tastiota increased inward, ranging from about 1.3 $\mu$g-at/l at the lagoon entrance to 10.1 $\mu$g-at/l at the head, an eight-fold in-

crease (Fig. 2B). Variations of total phosphate, from place to place as well as with time, paralleled variations of "turbidity." Most of the phosphate was present in the particulate form, either organically combined or inorganically adsorbed on suspended detritus. Its distribution, therefore, was strongly influenced by the total amount of materials in suspension.

Diurnal change of phosphate concentrations during a short period of wind-induced turbidity, generated by an afternoon seabreeze in the central lagoon, is shown by selected curves in Fig. 3. A rise in turbidity during the early afternoon was accompanied by an increase of total phosphate and by decreasing dissolved oxygen at a time when oxygen normally reaches a photosynthetic peak. Corresponding concentrations of inorganic phosphate varied within narrow limits with a slight decrease during the "turbid period" followed by a slight increase after the period.

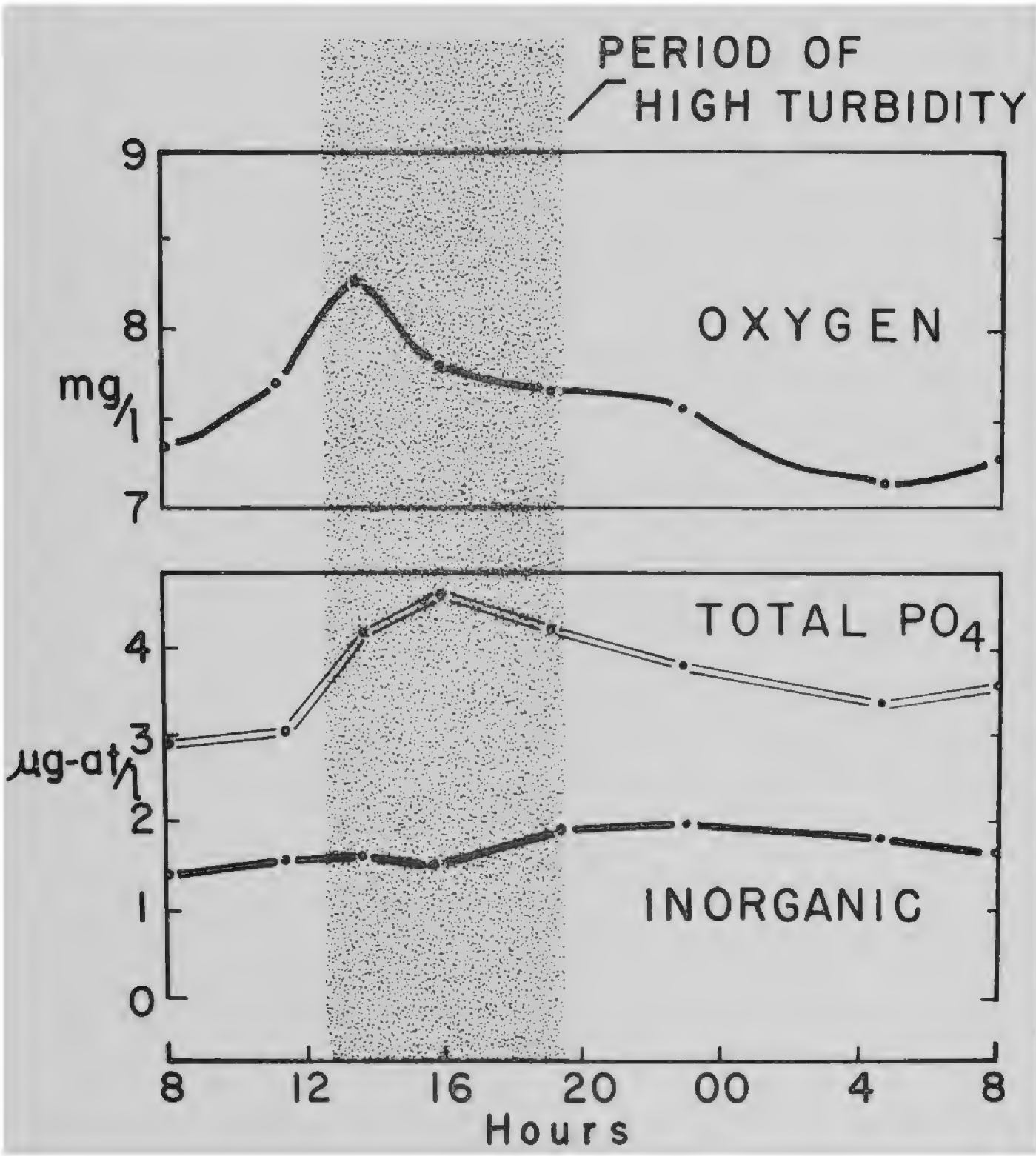


FIG. 3. Diurnal variations of dissolved oxygen and phosphate fractions showing effect of short-term wind-induced turbidity; central lagoon, Estero Tastiota, April, 1961.

Concentrations of "dissolved" phosphate also increased with distance headward ranging 0.9–1.4 μg-at/1 (Fig. 2B). Farther landward, in interstitial water about 1.2 m beneath the high flat surface, dissolved concentrations reached 8.2 μg-at/1. Phosphorus also increased upward in the near-surface sediments from 0.08 percent near the water table to 0.12 percent (total per dry weight of sediment) at the surface. These subsurface evaporative accumulations in the tidal flats largely are removed from further cycling in the lagoon system.

Data for production and respiration from varied environments are summarized in Table 1. Average rates of total free-water gross production, including the production of phytoplankton, reached 10.3 g $m^{-2}$ $day^{-1}$ in clear water off the tidal entrance; whereas, in the turbid central lagoon rates were 2.6 g $m^{-2}$ $day^{-1}$ (Fig. 2C). Gross production in bottles near the entrance reached more than 50 percent of the total gross production; whereas in the central lagoon this fraction amounted to less than 15 percent of the total, indicating a larger percentage of biological activity contributed by benthic organisms. Back channels and ponds enclosed by mangrove growths, are marked by comparatively large respiratory metabolism averaging 2.3 g $m^{-2}$ $day^{-1}$.

Average rates of free-water net production reached 1.9 g $m^{-2}$ $day^{-1}$ off the tidal entrance (Fig. 2D). The lowest rate, −0.9 g $m^{-2}$ $day^{-1}$ was measured in an inner embayment; the negative value indicates that community respiration exceeds photosynthesis. In Tastiota Deadwater, a turbid, brackish pond cut off from tidal influence, net production was −0.3 g $m^{-2}$ $day^{-1}$; whereas in the central lagoon, community respiration nearly balanced gross production and there was a substantial average net production of +0.4 g $m^{-2}$ $day^{-1}$. The rates of production in a single environment generally were lower in winter than in summer but the trend of relatively high values off the entrance and relatively low values in the central lagoon persisted from season to season. Production in comparable central reaches of nearby lagoons, Estero Soldado and Laguna Cardenal, attained net rates two to three times higher than at Estero Tastiota. These lagoons are less

TABLE 1

Values for Gross Production ($P_g$), Community Respiration (R), and Net Production ($P_n$), g $m^{-2}$ $day^{-1}$, from varied environments at Estero Tastiota, and nearby lagoons, Sonora, Mexico

| Location | Date | Light-Dark Bottle Method $P_g$ | R | $P_n$ | Free-Water Curve Method $P_g$ | R | $P_n$ | Water depth (m) |
|---|---|---|---|---|---|---|---|---|
| Nearshore gulf | Apr. 12–13, 1961 | 3.2 | 0.4 | +2.8 | 9.5 | 7.8 | +1.7 | 4.0 |
| | July 16–17, 1960 | 6.2 | 0.2 | +6.0 | 12.2 | 10.2 | +2.0 | .... |
| Central lagoon | Jan. 8– 9, 1961 | 0.1 | 0.1 | 0.0 | 1.7 | 1.4 | +0.3 | .... |
| | May 24–25, 1961 | 0.6 | 0.3 | +0.3 | 3.9 | 3.4 | +0.5 | 0.5–1.6 |
| | July 16–17, 1960 | 0.3 | 0.2 | +0.1 | 2.2 | 1.8 | +0.4 | .... |
| Inner embayment | Dec. 26–27, 1960 | 0.7 | 0.5 | +0.2 | 4.6 | 5.2 | −0.6 | 0.2 |
| | Apr. 12–13, 1961 | 0.6 | 0.3 | +0.3 | 5.2 | 6.0 | −0.8 | .... |
| | July 16–17, 1960 | 0.9 | 0.2 | +0.7 | 8.5 | 9.4 | −0.9 | .... |
| | July 9–10, 1960 | 0.9 | 0.4 | +0.5 | .... | .... | .... | .... |
| Deadwater | Mar. 22–23, 1961 | 0.3 | 0.4 | −0.1 | 0.7 | 1.0 | −0.3 | 0.2 |
| Mangrove pond | July 9–10, 1960 | 0.2 | 0.2 | 0.0 | 1.6 | 2.3 | −0.7 | 0.2 |
| | June 14–15, 1961 | .... | .... | .... | 1.1 | 2.3 | −1.2 | .... |
| Laguna Cardenal, central lagoon | June 20–21, 1960 | .... | .... | .... | 5.0 | 3.7 | +1.3 | 0.5 |
| Estero Soldado, central lagoon | Mar. 25–26, 1961 | 0.4 | 0.3 | +0.1 | 3.6 | 2.6 | +1.0 | 2.3 |

turbid than Tastiota, somewhat deeper in proportion to their areal extent, and contain larger communities of benthic grass.

## Discussion

### Phosphate

The supply and distribution of phosphate in lagoon water is regulated by processes of sedimentation inasmuch as this nutrient element occurs chiefly in the particulate form. Phosphate is ultimately derived from the land and from the gulf. The terrigenous-borne fraction consists of complex polyphosphates combined with clay minerals in calcareous soils of the region. A land source is shown by the relatively high content of phosphate in sediments at the entrance of dry rivers. Mineralogic analyses of these river-mouth sediments, as well as most surface sediments on the lagoon floor, indicate that both types are derived mainly from the land. Although imports of sediment into the lagoons are spasmodic and of short duration in the arid climate at present, nutrient-bearing sediments tend to deposit in the lagoons and remain there. Further, land discharge was more active in the recent past. Hutchinson (1957) reports high phosphate levels in inland saline lakes and enclosed basins of semi-arid regions. Rochford (1951) found relatively high levels of phosphate in the hypersaline estuaries of southwest Australia. Accumulations were attributed to intense local turnover and concentration against a gradient. By contrast, in some humid coastal lagoons, floods of low-nutrient fresh water tend to dilute, as well as flush-out, previously accumulated nutrients (Odum and Wilson, 1962).

Phosphate supplied to the lagoons from the gulf chiefly consist of particulate organic phosphate present in plankton and detritus. This relatively small increment is carried into the lagoons by flood flow or by the net inward flow of density currents, and eventually settles out in relatively quiet areas of the lagoon. Another part may accumulate near the head by the settling lag mechanism described by Postma (1961). Inward transport of gulf-derived organic materials is traced by the occurrence in the central lagoon of empty foraminiferal tests believed to be indigenous to the nearshore gulf.

The high inward gradient of total phosphate is attributed to a combination of processes that are intermittently active in the lagoon. Diurnal measurements of total phosphate showed that wave-stirring of the lagoon floor produced dense suspensions of bottom materials and corresponding high levels of phosphate. Similar trends were found in the deadwater where tidal action is absent. Inasmuch as the lagoon widens and shoals inward, agitation of the bottom is most effective in the broad inner reaches. Near the entrance wind-induced concentrations are reduced by mixing and exchange of lagoon water with relatively dilute gulf water. Near the head, settling in quiet embayments tends to reduce suspended concentrations, especially during calm periods; whereas transport by the settling lag mechanism favors headward concentration against the gradient. The small headward increase of dissolved phosphate is mainly attributed to evaporative concentration in the inner lagoon, but some phosphate may be released from reduced sediments during times of wave activity.

It is supposed that phosphate is rapidly recycled between water, sediments, and organisms. The variable character of the environment permits a wide variety of liberation and exchange phenomena to take place. Rapid turnover rates were observed by Bruce and

Hood (1959) in a study of diurnal variations in Texas bays. Liberation from the sediment may be effected by bacterial decomposition of entrapped organic matter. It is possible that release is aided by wave agitation which exposes anaerobic sediments beneath the thin oxidation-reduction layer. Part of the liberated phosphate may be adsorbed on sediment particles in overlying water and redistributed by sedimentary processes. Benthic plants, such as *Zostera*, rooted in anaerobic sediments, may directly take up phosphate. Baas Becking and Mackay (1956) called attention to the ability of *Enteromorpha* to accumulate phosphate.

## Organic Production

The broad range of values for production shows that organic matter is produced at different rates in different but interrelated environments of the lagoon system. Varied production rates are attributed partly to the different types of producers that inhabit the various environments and utilize the light and nutrients present. Phytoplankton production is important off the entrance, whereas benthic plant production dominates the lagoon proper. High rates of gross production in relatively clear water off the lagoon entrance, in contrast to low rates in the turbid central lagoon, also reflect differences in incident light reaching the producers. The influence of turbidity in depressing oxygen production is evident in diurnal variations of dissolved oxygen concentrations and corresponding turbidity measurements (*e.g.*, Fig. 3). In a study of lagoons on the Texas coast, Odum and Wilson (1962) demonstrated that the amount of adsorption and scattering by turbid materials controlled the photosynthetic output. Clear lagoons yielded greater production than turbid lagoons at the same light intensity. In Sonora, shading by suspended materials may be partly compensated by relatively high annual illumination which permits year-around production with successive populations.

Superimposed on the light-quenching influence of turbid materials, imbalances in lagoon metabolism arise from exchange of water and deposition of suspended detritus. In very shallow water, at the lagoon head and in the lower embayment, where turbid materials rapidly settle out, respiration was high and exceeded photosynthesis. This imbalance was probably due to the oxidation of organic detritus redistributed from the central lagoon where it was churned up by wave agitation. At the mouth, it is possible that gross production is stimulated by the alternate discharge of nutrient-rich lagoon water into the nearshore gulf.

When rates of gross production are compared to those studied in the Texas bays by Odum and Wilson (1962) using similar free-water methods, the Sonoran rates are generally lower for comparable environments. Levels of production in the central turbid reaches of Tastiota correspond to those of the "back bays" except for the slight predominance of photosynthesis over respiration. However, the scattered values for other Sonoran lagoons, Estero Soldado and Laguna Cardenal, are comparable to similar grass bottom environments in San Antonio Bay, Texas.

Most of the organic material produced in the lagoon at Tastiota is decomposed prior to permanent burial. In the central lagoon, for example, average net production is about 0.4 g $m^{-2}$ $day^{-1}$ or 146 g $m^{-2}yr.^{-1}$ and the surface sediments average 0.34% organic carbon or about 0.62% organic matter. With a sedimentation rate of 0.08 cm $yr^{-1}$ and an average sediment density of 2.65, organic matter accumulates on the lagoon floor at a rate of 14.42 gms $m^{-2}$ $yr^{-1}$. This is only 9% of the total organic matter produced. Ad-

ditional losses occur after deposition; at 10 cm only about 3.4% of the organic matter produced remains. The estimate reveals the great loss of organic matter from the time it is produced until it is permanently deposited. Accordingly considerable regeneration of nutrients must take place within the sediments.

## Summary

Phosphate, present chiefly in the particulate form, is derived from land drainage and partly from the sea. In the lagoon, suspended phosphate concentrations are redistributed by a variety of processes that lead to a high headward gradient paralleling turbidity. Phosphate-enriched suspensions, produced largely by wave-agitation of the lagoon floor, may accumulate toward the head by inward transport of tidal flow. Settling of suspended materials and mixing with dilute gulf water tend to level the gradient.

Variations of production from place to place reflect variations of turbidity and the activity of different types of producers. Phytoplankters are important producers off the entrance and benthic grasses are significant in the lagoon proper. Wind-induced turbidity of the central lagoon retards rapid photosynthesis and leads to a near balance between community respiration and gross production; whereas, off the lagoon entrance, better light penetration results in excess photosynthesis and substantial net production.

## Acknowledgments

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# Surface Salinities for Baffin Bay and Laguna Madre, Texas April 1964–March 1966

E. William Behrens

## Abstract

Surface salinities through the upper Laguna Madre and Baffin Bay were taken from April, 1964 through March, 1966 and span a transition from a very dry period to a year with normal rainfall. The data suggest that maximum salinities under drought conditions probably do not exceed 85 ppt. in Baffin Bay and 75 ppt. in Laguna Madre; under normal conditions Laguna Madre's salinity is between 30 and 40 ppt. and Baffin Bay's is between 40 and 50 ppt.

## Introduction

The characteristics of the Recent sediments at any particular place are the results of many decades of deposition and thus usually reflect average environmental conditions. The distribution of these characteristics, therefore, should not be correlated with environmental conditions such as salinity as they exist at any one time. The purpose of this study is to determine the average or normal state of surface salinities in two hypersaline bays and the extent of their fluctuations.

Baffin Bay and Laguna Madre, Texas are separated from the Gulf of Mexico by Padre Island. They have average depths of 5.0 and 3.3 feet, respectively, and maximum depths of 10 feet. Sea water enters these bays from the Gulf through Brazos Santiago and Port Mansfield channels 75 and 45 miles, respectively, south of the mouth of Baffin Bay and Aransas and Corpus Christi Passes (the latter closed since about 1900) 40 and 23 miles, respectively, to the north. The predominating southeasterly winds generate northward flowing currents from the southern passes through the intracoastal canal which has connected northern and southern Laguna Madre since 1949. Previous to this date exchange with the Gulf was through only the northern passes and occasional hurricane washovers. Lunar tides are small, but notable fluctuations occur during seasonal tides. Run-off water enters Baffin Bay through only a few intermittent streams; no streams enter Laguna Madre. Evaporation exceeds precipitation by about 24 inches annually. Further details concerning the hydrography and meteorology of this area are given by Collier and Hedgpeth (1950) and Simmons (1957).

The depositional environments in Baffin Bay and Laguna Madre are characterized most distinctively by restricted faunas and carbonate precipitation (chiefly in the form of oolitic beach sands). Hypersalinity is, to a large extent, responsible for these characteristics (Pearse and Gunter, 1957; Simmons, 1957; Dalrymple, 1964; Behrens, 1964). Consequently, when sedimentary structures, petrography, or shell assemblages similar to those now found in Baffin Bay and Laguna Madre are observed in either Recent sediments or ancient strata, one can conclude that the original depositional environment was hypersaline (*e.g.*, Behrens, 1965a). It would be desirable, however to be able to be more specific, *i.e.*, to be able to distinguish between sediments deposited at different degrees of hypersalinity. Baffin Bay and Laguna Madre are being studied, because salinities therein vary from below normal marine to over 70 ppt.

## Methods and Results

Salinities of surface waters were determined monthly from April, 1964 through May, 1966 with a Goldberg Refractometer (Behrens, 1965b) along a traverse extending from Intracoastal Waterway marker one at the southern end of Corpus Christi Bay through the upper Laguna Madre to the mouth of Baffin Bay (marker 122) and thence along the marked channel through Baffin Bay into the western arm, Laguna Salada (total 27 stations; Fig. 1). Although bay-center, surface salinities hardly define the salinity regime for the entire bays, they differ very little and are thus representative of the salinities along the beaches and in most shallow, bay-margin areas where almost all of the benthos dwell and where the carbonate precipitation occurs. From the plotted traverses (Fig. 2) an average salinity was determined graphically for each bay for each month. Salinities in Laguna Madre are characteristically lower than in Baffin Bay, because Laguna Madre water is diluted by water entering from the southern Laguna during southeasterly winds and from Corpus Christi Bay during north winds. During the summer months northerly currents also displace the saltiest water in the Laguna Madre from the mouth of Baffin Bay northward. Surface salinities at the northern end of the Laguna Madre are often low because the denser, northward-flowing, saline water flows under the lighter Corpus Christi Bay water which forms a fresher wedge at the surface (Collier and Hedgpeth, 1950, p. 169, Fig. 28).

Monthly and annual rainfall data were obtained from the U. S. Weather Bureau

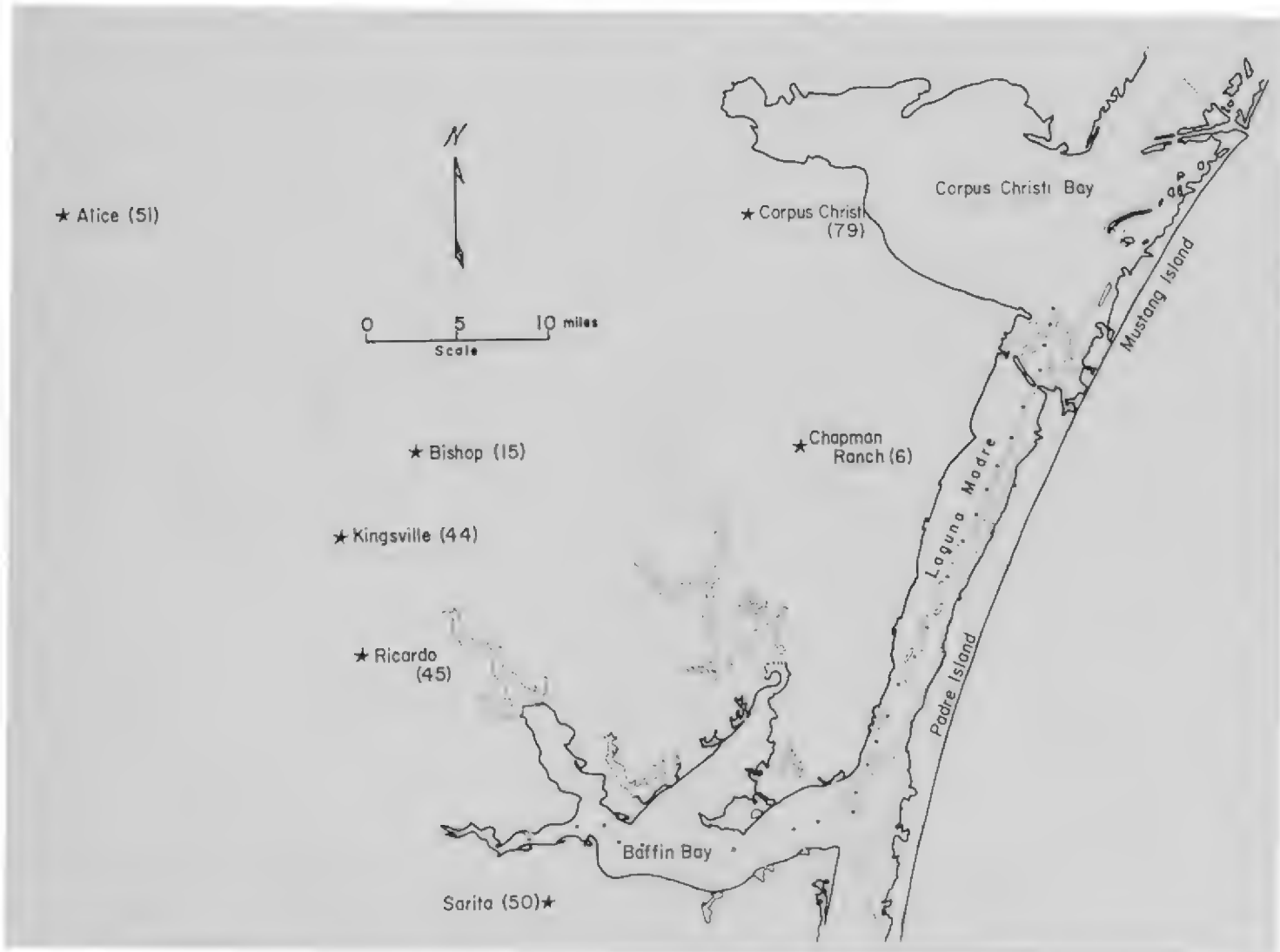


FIG. 1. Index map showing U. S. Weather Bureau Stations and years of record (in parentheses). Surface salinity stations along Intracoastal Waterway and Baffin Bay channel are indicated by small stars.

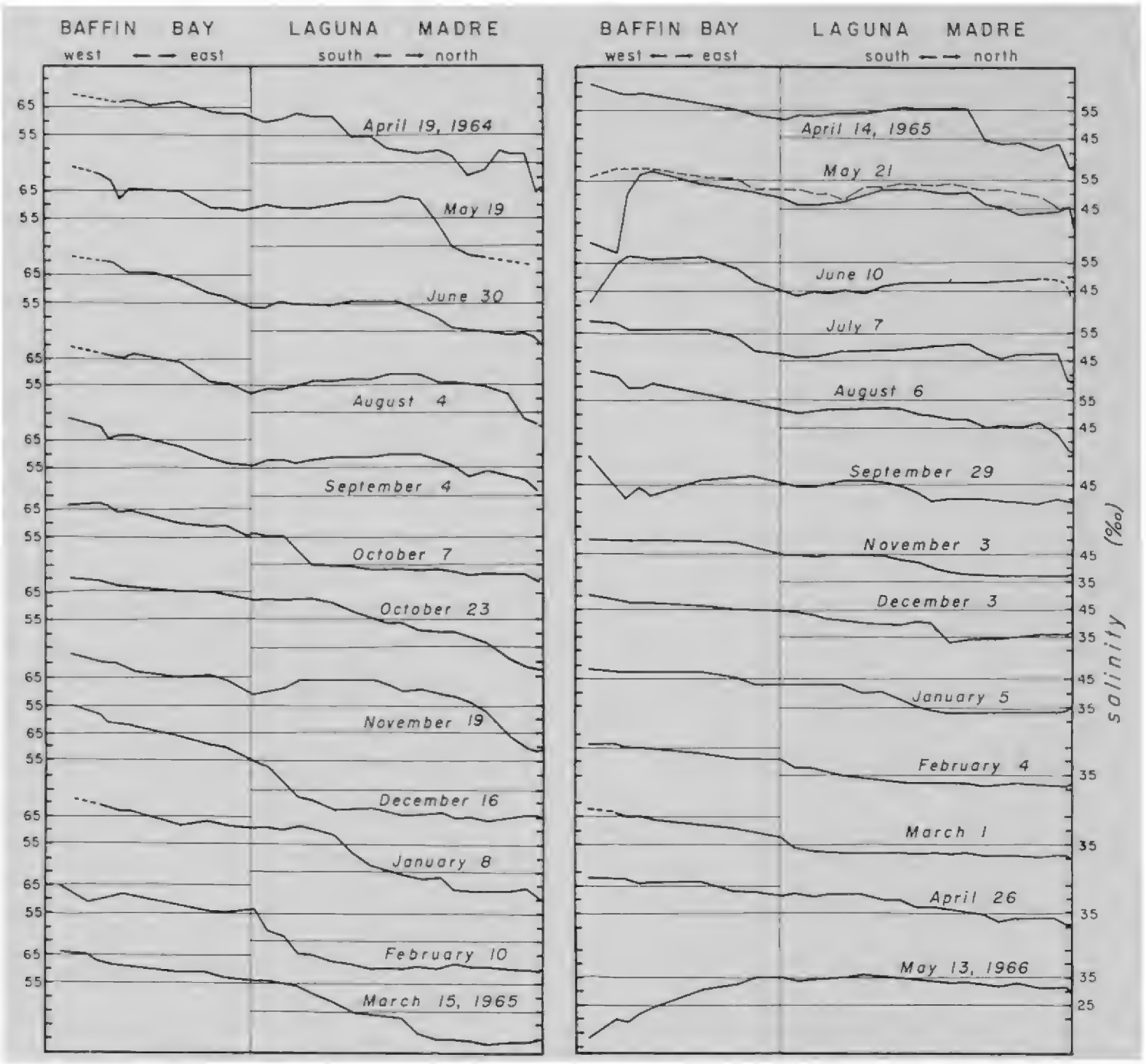


FIG. 2. Surface salinities. All salinities are for surface water except May 21, 1965, where dashed line indicates bottom water. Line of traverse indicated in Fig. 1.

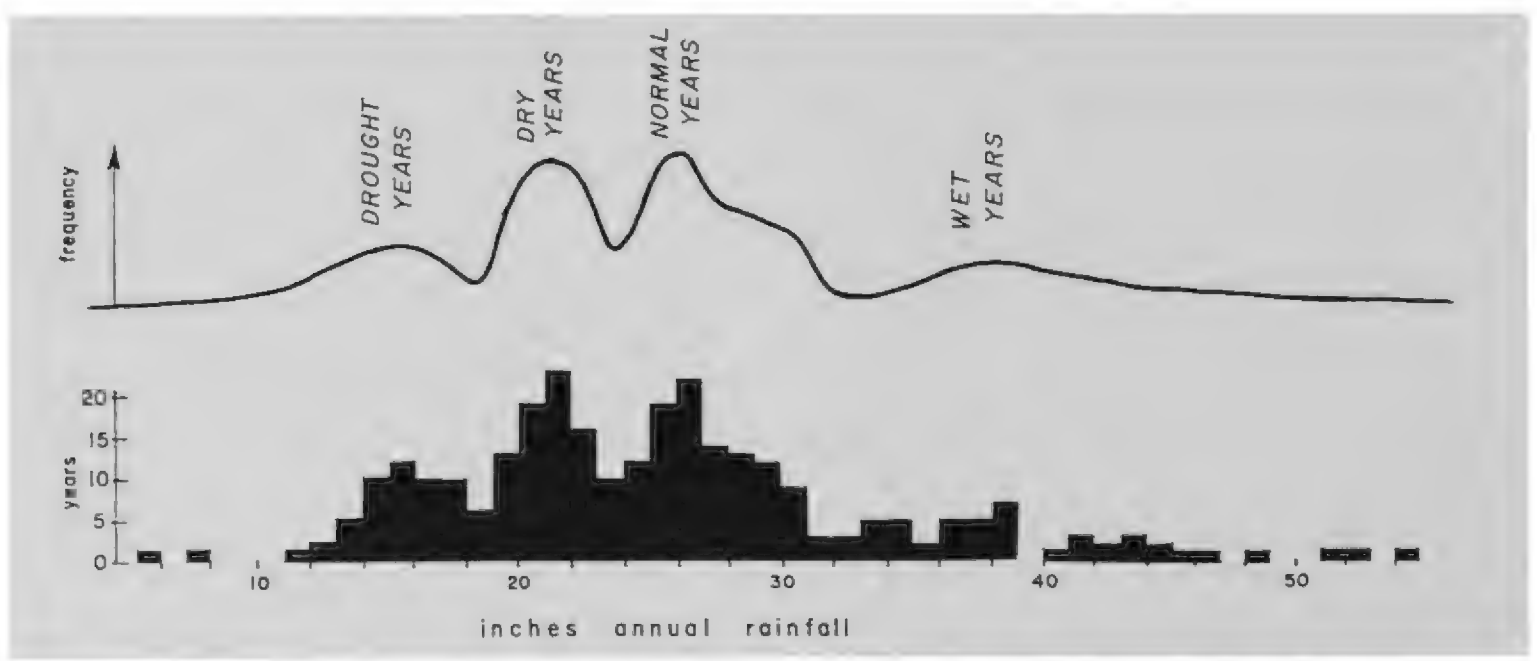


FIG. 3. Distribution of annual rainfall for 290 record years for stations shown on Fig. 1.

Climatological Data, Texas Section, for the seven stations shown on Fig. 1. Average annual rainfall for all stations (total 290 record years) is 25.3 inches. Four modes are apparent in the yearly distribution of rainfall (Fig. 3). These are designated: drought years—below 19 inches (20%); dry years—19 to 24 inches (28%); normal years—24 to 32 inches (35%); and wet years—above 32 inches (17%).

Monthly distribution of rainfall is illustrated in Fig. 4. The climate is characteristically dry with brief periods of heavy rain which may occur in any month but most commonly fall in May and September. These are the only two months in which rainfalls of more than 2 inches are more common than rainfalls between one and two inches. This dry or wet phenomenon is reflected in the monthly precipitation records for April, 1964 through May, 1966 which show that rainfall was either less than one inch or more than two inches in all but three of the 24 months and was between two and three inches for only four months (Fig. 5).

The surface salinity averages over this same period show fairly close response to the monthly deviations from average rainfall (Fig. 5). Discrepancies are accounted for, at least in part, by the nonrepresentativeness of the data. Rain is commonly localized in thunderstorms, and monthly differences between nearby stations of over five inches have been recorded. Surface salinities are often low, because following rains the bays are often stratified with lighter, fresher water overlying denser salt-water (Fig. 2).

## Discussion

From the climatological data we can predict a surface salinity regime for normal years (Fig. 5). In Baffin Bay there should be no increase in salinity during the winter months

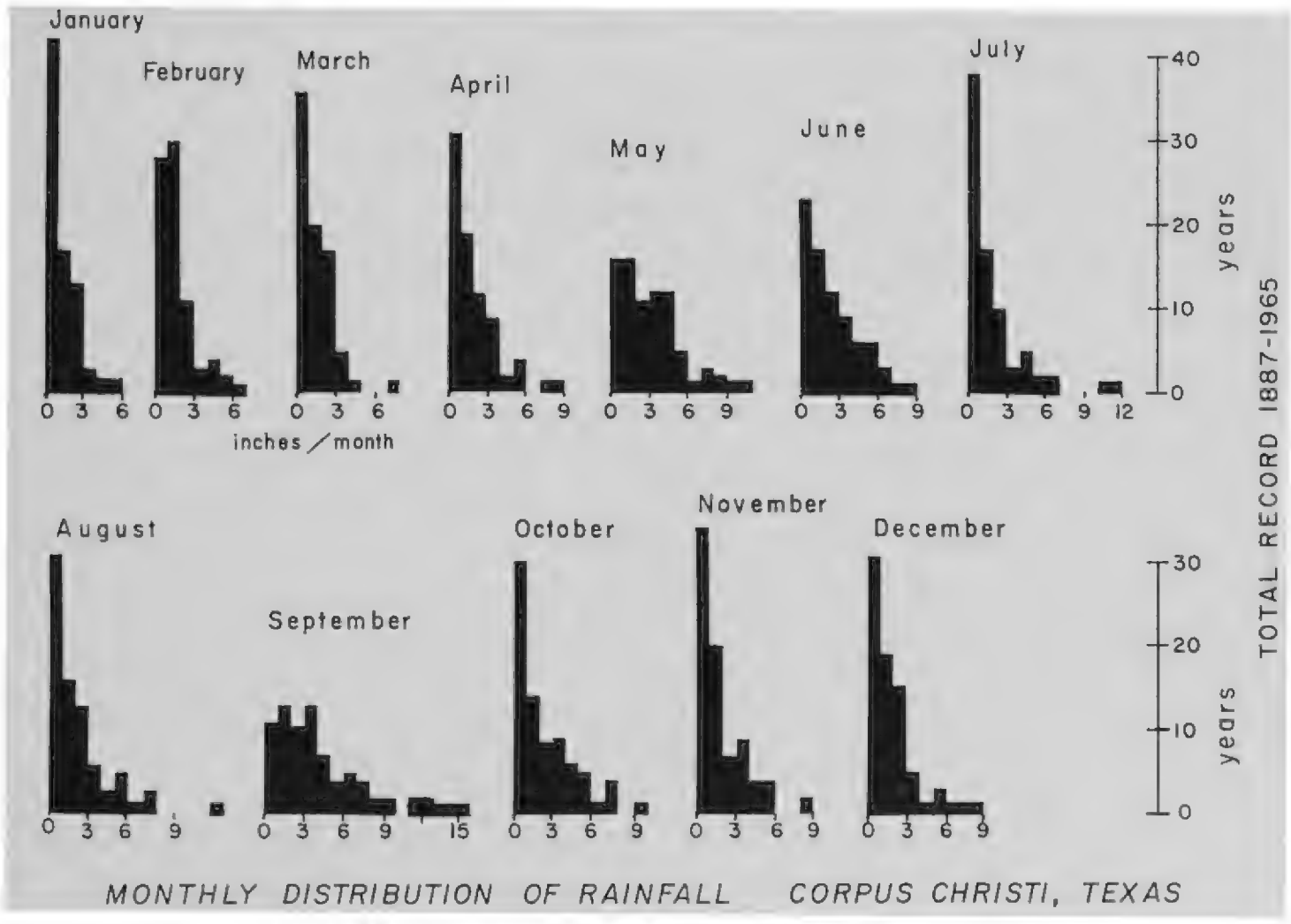


FIG. 4. Monthly rainfall, Corpus Christi, Texas; 79 record years.

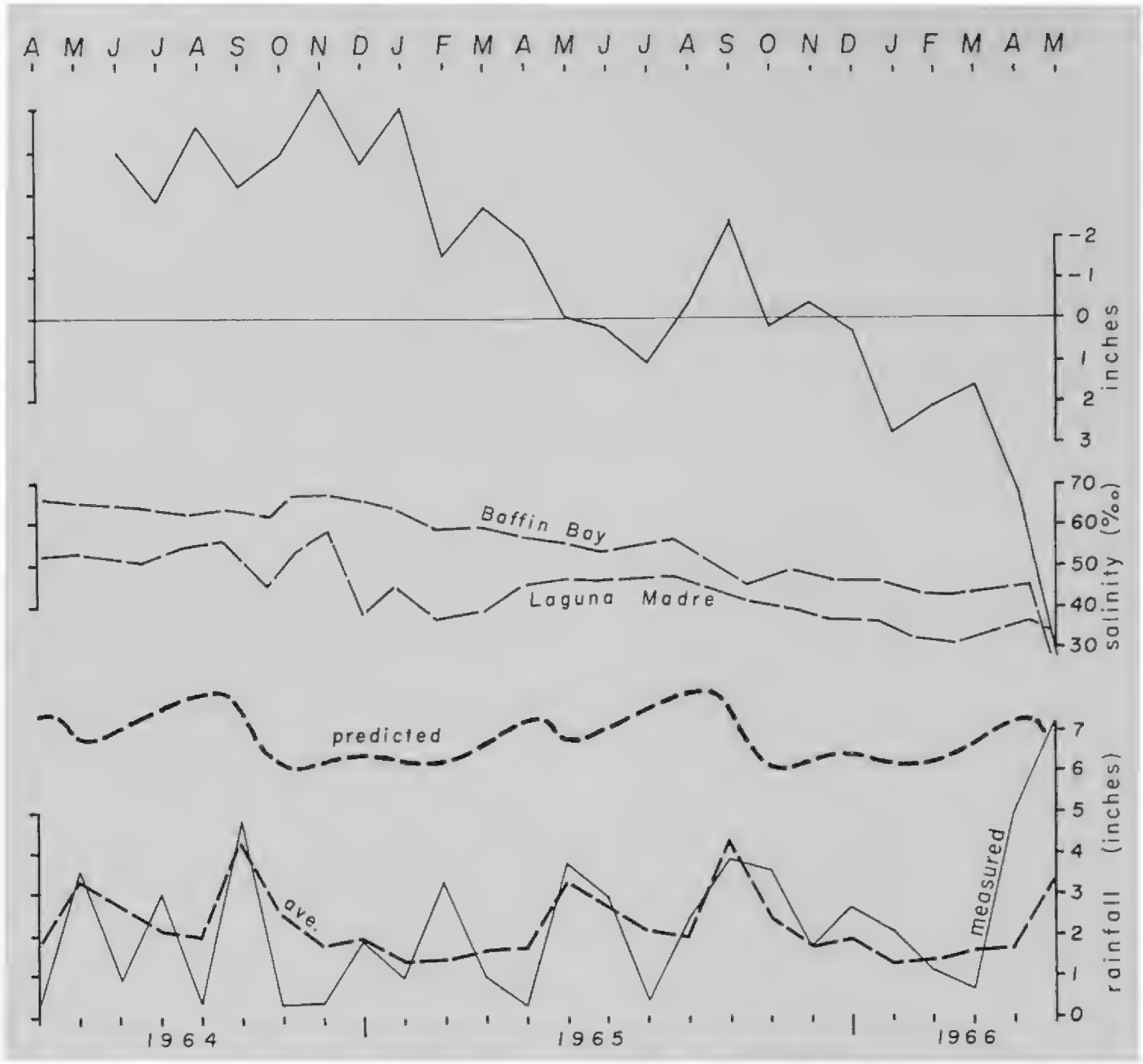


FIG. 5. Salinity and rainfall data for April, 1964 through May, 1966. From bottom to top; monthly rainfall averages—heavy dashed line; measured monthly rainfall—lighter, solid line; normal salinity changes predicted from average rainfall curve; graphically averaged surface salinities for Laguna Madre and Baffin Bay; departure from average rainfalls for six month totals. Climatological data for 1964 and 1965 are from all stations shown on Fig. 1; data for 1966 from Corpus Christi only.

of December, January, and February, because although rainfall is low, evaporation is at a minimum. The greatest seasonal low tide is usually in February. By the end of March increasing sunshine, temperatures, and consequent evaporation should cause a salinity increase. This increase is small at first, because a spring high tide replaces the winter low and brings in Gulf water, but the increase accelerates through April until the May rains drop it again. A steady increase should ensue through the summer months of June, July, and August due to little rainfall, a high evaporation rate, and low tides until the September rains and fall high tides cause another, larger drop. Continued warm temperatures and decreased rainfall should cause a small increase in the fall through October and November until the northers become frequent in December and a leveling or slow decrease begins again.

The 1965 salinities follow this prediction except for a spring decrease and a subdued summer increase. These two anomalies contributed largely to a year-long decrease in surface salinities. This decrease was probably in response to a change from drought years

in 1962 (16.7″), 1963 (15.8″), and 1964 (18.5″) to a normal rainfall year in 1965 (26.1″). In these circumstances any months with above average or even average rainfall, *e.g.*, July and December, 1964, February, August, October, and December, 1965, would tend to subdue normal increases and intensify decreases. Apart from this, the chief departure of the Baffin Bay curve from the predicted curve is a larger than normal fall (1964) surface salinity increase due to exceptionally dry October and November.

The Laguna Madre differs from Baffin Bay in that in the Laguna there is a larger drop in surface salinities during the winter months (Fig. 5), because of north winds pushing the saltier water into the southern Laguna Madre and fresher Corpus Christi Bay water into the northern Laguna (Simmons, 1957).

During dry and drought years the spring and fall decreases probably do not take place or are subdued, and salinities rise throughout the year. Although circulation in these bays is restricted, it was increased by the dredging of the Intracoastal Waterway which eliminated a sill effect at the north end of Laguna Madre. Thus exchanges with the marine waters of the Gulf of Mexico will probably prevent salinities from exceeding about 85 ppt. in Baffin Bay and 75 ppt. in Laguna Madre except, of course, in very restricted marginal areas such as tidal pools.

During wet years sharp drops in salinity may occur during any month to the extent that the surface waters of the bays may become brackish.

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